

Insects of the Yukon: Characteristics and History

H.V. DANKS

Biological Survey of Canada (Terrestrial Arthropods), Canadian Museum of Nature
P.O. Box 3443, Station "D", Ottawa, Ontario, Canada K1P 6P4

J.A. DOWNES

Canadian Museum of Nature
P.O. Box 3443, Station "D", Ottawa, Ontario, Canada K1P 6P4

D.J. LARSON

Department of Biology, Memorial University of Newfoundland
St. John's, Newfoundland, Canada A1B 3X9

and

G.G.E. SCUDDER

Department of Zoology, University of British Columbia
6270 University Blvd., Vancouver, British Columbia, Canada V6T 1Z4

Abstract. The Yukon Territory provides a setting for its fauna of particular historical and ecological interest. Much of the Yukon was unglaciated in Pleistocene time as part of Beringia, a much larger ice-free but essentially treeless area extending through Alaska into eastern Siberia, and this whole area was cut off from the rest of North America by ice sheets. After deglaciation the Yukon was again connected to the North American continent, allowing for movements by and contacts with other faunas. The Yukon today is a distinctly northern region dominated by arctic, alpine, subarctic and boreal terrain. Nevertheless, it is relatively benign for its latitude of 60–69°N, and habitat diversity is enhanced by the local amelioration of temperature on south-facing slopes and in river valleys.

As a result of these past and current influences, the insect fauna of the Yukon is relatively rich and distinctive, reflecting the results of evolution on a variety of scales, and comprising distinctive forest, grassland, tundra and other species. The composition of the fauna reflects the current or past prevalence of particular habitats, such as boreal forest (which supports many widely distributed North American species), shallow still waters (which support many aquatic species) and dry grasslands on warm slopes (which support many leafhoppers and heteropterans, for example). The groups reported on in this book contain about one third of the known arachnid fauna of Canada and more than half of Canada's insect fauna. In these groups, 297 species of spiders, 157 species of mites, and 2711 species of insects—or about one fifth of the Canadian species known in those groups—are recorded in the Yukon, suggesting that in total more than 6000 species of insects and 900 species of arachnids occur there. Individual species as well as different groups differ widely in ecological and distributional features according to their particular histories. However, the fauna, like the terrain, is distinctly northern; it is dominated by certain northern and widespread taxa, whereas other groups are represented by few species. The prevalence of northern groups tends to be correlated, though by no means exclusively, with their occupation of aquatic habitats (relatively favourable in the north) and with general feeding habits such as predation (relatively advantageous where specific resources are more limited). Many adaptations of structure, behaviour and life-cycle reflect the demands of cold and seasonal life zones.

Overall, nearly twice as many Yukon species of insects are restricted to the Nearctic region as occur in both Nearctic and Palaearctic regions, though a few northern groups, as well as spiders and oribatid mites, have many Holarctic species. Much taxonomic evidence, such as the occurrence of sister species in the Yukon and in Asia, indicates past connections between North America and Eurasia that preceded the well known Pleistocene connection.

About half of the Nearctic species of the Yukon are widespread in North America, and one third are western. These and other ranges suggest that species have come to occupy the Yukon by several different routes. For example, northern boreal ranges predominate among the Nearctic species. Therefore, many of them probably are postglacial invaders from the south and east. However, other widely distributed arctic and boreal species are known from Beringia as Pleistocene fossils, reflecting their presence there during glaciation. Several species appear to have survived the Pleistocene in both Beringian and southern refugia, because they have distinct or disjunct northern and southern populations. In several groups substantial numbers of species occur only in the (glaciated) southern parts of the Yukon and have not spread farther north; they are presumed to have entered the Yukon from the south after

deglaciation. Also presumed to be invaders from the south after glaciation are species, especially from stream habitats, that range from the Cordillera into the Yukon but are restricted to the southern Yukon.

About a tenth of the insect species in the Yukon are restricted to the northern unglaciated areas in North America, suggesting that these species survived the ice-age in Beringia but have not subsequently spread beyond it. These species occur in East Beringia only, across Beringia, or in the Palaearctic region plus East Beringia, but not more widely in the Nearctic region. The habitat requirements of the species confined to Beringia indicate the existence there in the Pleistocene of dry grassland, tundra and other habitats.

Additional evidence, grounded in wider collecting and systematic study, is required to analyze the dynamics of colonization and faunal interactions in the Yukon, and to establish the reasons for the continuing limitation of some species to Beringia. Although some evidence suggests that the fauna is more or less integrated, it may not yet have reached full equilibrium with climatic and biotic influences following deglaciation. In any event, the taxonomic and ecological structure of the Yukon insect fauna continues to demonstrate the constraints of current environments and the repercussions of Beringian history.

Résumé. *Les insectes du Yukon: caractéristiques et historique.* La situation du territoire du Yukon rend l'étude de sa faune particulièrement intéressante des points de vue historique et écologique. Le Yukon, resté pour une grande part dénué de glaces au cours du Pléistocène, faisait partie de la Béringie, un territoire non englacé beaucoup plus vaste s'étendant jusqu'en Sibérie orientale en passant par l'Alaska et coupé du reste de l'Amérique du Nord par les glaces. Après les glaciations, le Yukon a été de nouveau relié au continent nord-américain, donnant lieu à des déplacements d'espèces et recréant des liens avec d'autres faunes. Aujourd'hui, le Yukon est une région essentiellement nordique dominée par des zones arctiques, alpines, subarctiques et boréales. Cependant, son climat est relativement doux pour cette latitude (60–69°N) et la diversité des habitats est accentuée par les conditions de température particulièrement clémentes des adrets et des vallées.

La faune d'insectes qui résulte de ces influences passées et présentes est relativement riche et distinctive et on y reconnaît les résultats de l'évolution qui a agi à diverses échelles, soit des espèces des forêts, des prairies herbeuses, de la toundra, etc. La composition de la faune est reliée à l'existence présente et passée d'habitats particuliers, forêt boréale (qui supporte plusieurs espèces très répandues en Amérique du Nord), eaux stagnantes peu profondes (où vivent de nombreuses espèces aquatiques) et zones herbeuses sèches sur les adrets (qui abritent entre autres de nombreuses espèces de cicadelles et de punaises). Les groupes dont il est question dans ce livre contiennent environ le tiers des espèces connues d'arachnides au Canada et plus de la moitié de la faune canadienne d'insectes. Chez ces groupes, 297 espèces d'araignées, 157 espèces d'acariens et 2711 espèces d'insectes—soit environ le cinquième des espèces canadiennes connues dans ces groupes—ont été trouvées au Yukon, ce qui permet de croire qu'au total plus de 6000 espèces d'insectes et plus de 900 espèces d'arachnides vivent au Yukon. Les espèces et les divers groupes ont des caractéristiques écologiques et zoogéographiques très disparates qui reflètent l'histoire particulière de chacun. Cependant, la faune, comme d'ailleurs l'environnement, est distinctement nordique: elle est dominée par certains taxons nordiques ou à vaste répartition, alors que d'autres groupes ne sont représentés que par quelques espèces. La prédominance des groupes nordiques a tendance à être associée, pas exclusivement cependant, à l'occupation d'habitats aquatiques (milieux plutôt favorables dans le nord) et à des habitudes alimentaires généralistes comme la prédation (une stratégie relativement efficace aux endroits où certaines ressources particulières sont limitées). Plusieurs des adaptations morphologiques, comportementales et démographiques reflètent les conditions particulièrement rigoureuses des zones froides et saisonnières.

Dans l'ensemble, il y a au Yukon près de deux fois plus d'espèces d'insectes restreintes à la zone néarctique que d'espèces qui habitent à la fois la zone néarctique et la zone paléarctique, bien que quelques groupes nordiques d'insectes, de même que d'araignées et d'oribates, comptent plusieurs espèces holarctiques. Plusieurs indices de nature taxonomique, par exemple la présence d'espèces soeurs au Yukon et en Asie, reflètent l'existence de contacts entre l'Amérique du Nord et l'Eurasie bien avant celui du Pléistocène.

Environ la moitié des espèces néarctiques du Yukon sont répandues dans toute l'Amérique du Nord et un tiers font partie de la faune de l'ouest, ce qui suppose que le Yukon a été colonisé par des espèces qui ont suivi des voies diverses. Par exemple, les espèces néarctiques ont surtout des répartitions boréales nordiques; plusieurs d'entre elles ont donc probablement envahi le Yukon après les glaciations à partir de localités plus australes ou plus orientales. De plus, d'autres espèces arctiques et boréales fossiles du Pléistocène, bien répandues, ont été trouvées en Béringie, ce qui prouve leur présence dans cette zone durant les glaciations. Plusieurs espèces semblent avoir survécu au Pléistocène aussi bien en Béringie que dans des refuges plus austraux, puisqu'elles ont des populations distinctes ou discontinues dans le nord et dans le sud. Chez plusieurs groupes, bon nombre d'espèces ne vivent que dans la partie sud du Yukon (englacée) et ne se sont pas répandues plus au nord; il semble qu'elles soient parvenues au Yukon à partir de localités plus australes après la disparition des glaces. Sont aussi présumées avoir envahi le Yukon à partir du sud après les glaciations, des espèces, particulièrement des espèces d'eau courante, que l'on retrouve de la Cordillère au Yukon mais qui sont restreintes à la partie sud du Yukon.

Environ le dixième des espèces d'insectes du Yukon sont restreintes aux zones non englacées du Yukon en Amérique du Nord, ce qui semble indiquer que ces espèces ont survécu aux glaciations en Béringie, mais ne se sont pas répandues au-delà après la disparition des glaces. On les retrouve en Béringie orientale seulement, ou dans toute la Béringie, ou dans la région paléarctique et en Béringie orientale, mais pas au-delà dans la zone néarctique. Les besoins environnementaux des espèces confinées à la Béringie indiquent qu'il existait déjà, au Pléistocène, des plaines sèches, des zones de toundra et d'autres habitats.

Des échantillonnages plus poussés et des études systématiques s'imposent avant qu'il ne soit possible de faire l'analyse de la dynamique de la colonisation et des interactions fauniques au Yukon et d'établir les raisons du confinement de certaines espèces à la Béringie. Bien que la faune soit déjà plus ou moins intégrée, il est possible que l'équilibre entre la faune et les influences climatiques et biotiques après le départ des glaces ne soit pas encore tout à fait atteint. Il n'en reste pas moins que la structure taxonomique et écologique de la faune des insectes du Yukon continue de mettre en lumière les contraintes imposées par l'environnement actuel d'une part et, d'autre part, les répercussions de l'histoire de la Béringie.

Table of Contents

	Page
Introduction	965
The Information Available	968
Strengths of the Data	968
Weaknesses of the Data	969
Taxonomic Patterns	970
Number of Species and North American Comparisons	971
Comparison with Adjacent Areas	975
Composition of the Fauna	976
Variation	978
Wing Loss and Other Structural Modifications	978
Ecological Patterns	979
Habitats	980
Trophic Relationships and Biological Interactions	982
Adaptations	984
Ecological Correlations	987
Distributional Patterns	989
Synopsis of Ranges	993
Nearctic Ranges	995
Beringian Ranges and Beringian Extensions	996
Ranges Excluding Beringia	997
Disjunct Ranges	997
Zonal/Habitat Ranges	997
Status and Development of the Yukon Fauna	999
Kinds of Evidence	999
Past Conditions and Glaciation	999
Beringian Habitats	1001
Barriers and Dispersal	1003
Taxonomic Evidence	1004
Range Types	1005
Post-Pleistocene Development of the Fauna	1006
Conclusions	1007
Future Prospects	1010
Acknowledgements	1010
References	1010

Introduction

The arthropod fauna of the Yukon Territory is both fascinating and instructive. The area has long been a touchstone for northern biogeographers because it was not glaciated during the Pleistocene (Matthews 1979), and many species of plants (e.g. Cody 1971) and animals (e.g. McPhail and Lindsey 1970) survived glaciation there. Moreover, current mainland life zones in northwestern North America are relatively rich for their latitude, for example supporting boreal forests even at 64°N at lower elevations. In contrast, sites at 60°N, the latitude of the southern Yukon, are distinctly arctic in eastern North America. The Territory thus provides a setting for the fauna of particular ecological and historical interest (Downes 1997; Schweger 1997; Scudder 1997*a*).

From an historical perspective, 3 features of Pleistocene time in the Yukon are especially noteworthy. First, much of the area was unglaciated. Second, unglaciated areas extended

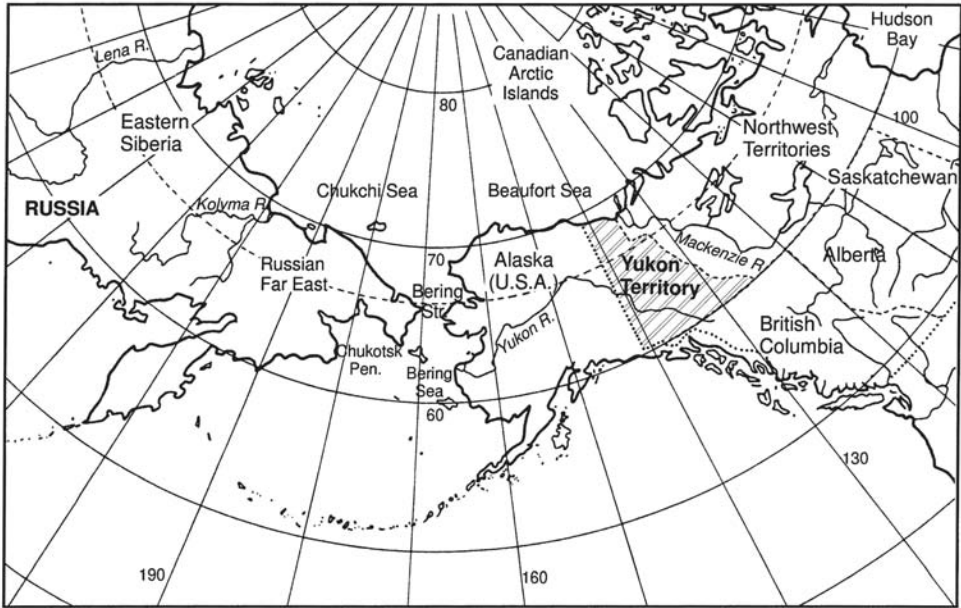


FIG. 1. Map of the Yukon Territory and surrounding areas.

through Alaska to eastern Siberia across what is now Bering Strait. Third, these territories were cut off from the rest of North America by ice sheets on the east and the south. Such an unusual combination of features gave rise to the general geographic concept of Beringia, referring to the northern unglaciated lands between the Lena River on the west and the Richardson and Mackenzie Mountains along the Yukon border on the east (compare Fig. 1; Wiggins and Parker 1997, fig. 16). However, the concept of Beringia is not restricted to a particular time or implying a particular sea level (Matthews and Telka 1997). Since deglaciation, the area has been connected to the rest of North America (but largely cut off from Eurasia), allowing contact to the east with deglaciated lands across northern North America, and to the south especially with montane or Cordilleran faunas.

From a current perspective, notwithstanding the amelioration of northern climates in western North America compared to the east, the Yukon is clearly northern. The bulk of the area is a subarctic plateau interspersed with mountains (cf. Fig. 2): all areas except the main river valleys are above 600 m, and one-third of the area is above about 1500 m. Consequently, about 40% of the area is treeless. At the northern fringe of this subarctic plateau, beyond the British Mountains, is an arctic coastal strip. At the southern end are rich river valleys, especially in the moister east (e.g. the Liard River). This southern aspect persists locally to the north, especially along the rivers, because the major valleys are deeply cut to lower elevations, and even in the north are relatively wide. The geological structure, though complex, trends northwest-southeast, causing the valleys to have sun-warmed, dry south-facing slopes that support a characteristic flora and fauna. The soils of the plateau are relatively fertile because they were not denuded of soil by glaciation. These features have made available a great diversity of terrestrial and aquatic habitats for insects (see Habitats below).

These past and current features of the Yukon Territory make it a key area for biogeographical study of northwestern, Canadian and North American faunas. In the Yukon,

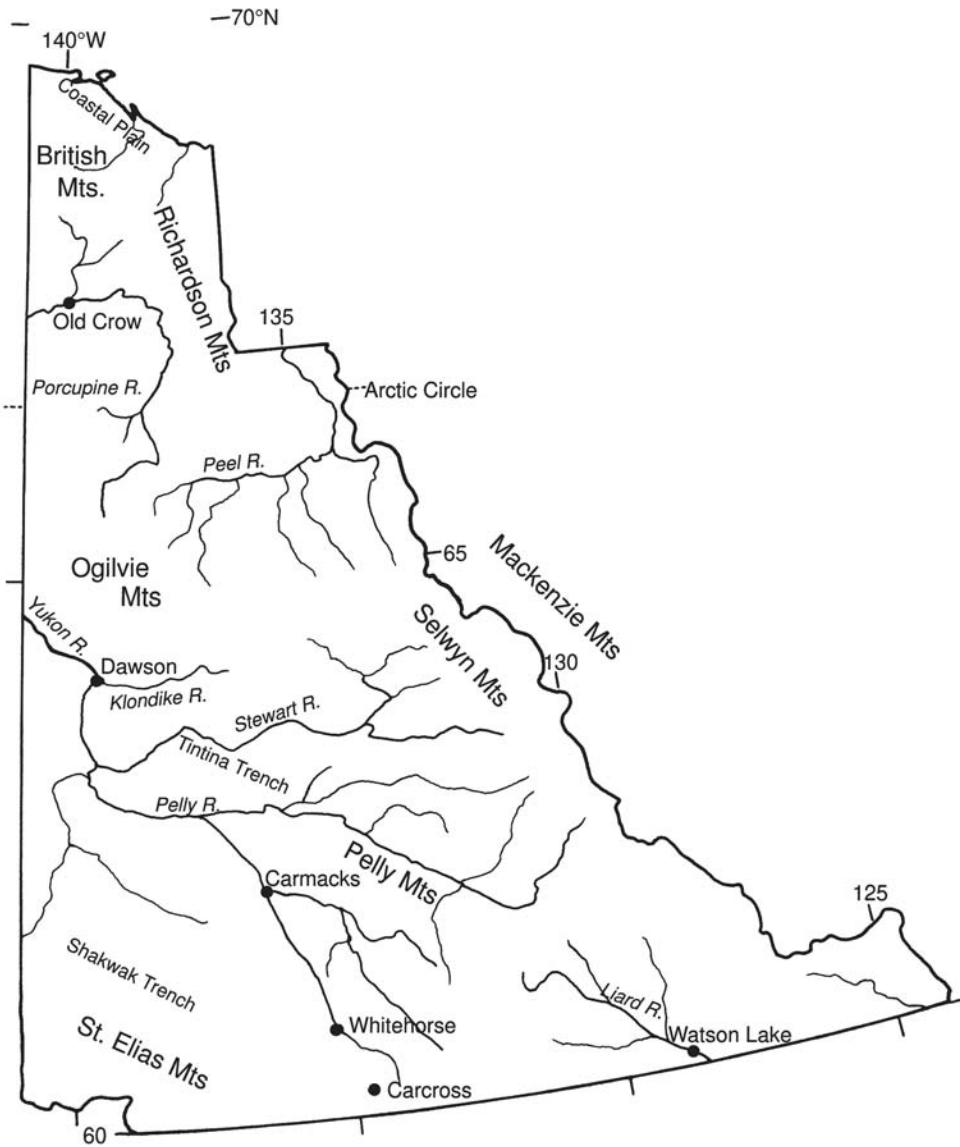


FIG. 2. Map of selected features of the Yukon.

the results of environmental change, dispersal, colonization and evolution on a variety of scales have been captured in the patterns of diversity and ecology of the fauna. This chapter outlines the nature of this fauna, summarizes some key elements of its diversity and ecology, and considers its origins and development; to do so it emphasizes the detailed information presented elsewhere in this book, much of which is new but some of which is based on earlier publications cited by the individual authors.

The extent and reliability of data available for this purpose are first discussed. Based on the data and their interpretations provided by chapter authors about numbers of species,

faunal composition, ranges, habitats and other biological features, tabular summaries are used to identify characteristic taxonomic, ecological and distributional features of the Yukon fauna. A final section reviews the kinds of evidence from which biogeographical conclusions can be drawn, and attempts a synopsis of the nature and development of the Yukon fauna.

The Information Available

Strengths of the Data. The documentation and taxonomic information summarized in earlier chapters is an essential basis for study of the Yukon fauna. Careful taxonomic work, including extensive and necessary comparisons of specimens from the Old World and elsewhere, have allowed interesting issues of synonymy, variation, and so on to be explained by Behan-Pelletier (1997), Cannings (1997), Larson (1997), Marshall (1997), Oliver and Dillon (1997), Wiggins and Parker (1997), and others.

Substantial information on the Yukon fauna has been organized by authors of individual chapters into annotated lists, which reveal how substantial are the additions to our knowledge of the fauna of the area. For example, three-quarters of the named chironomid species reported here by Oliver and Dillon (1997) and many of the sphaerocerids reported by Marshall (1997) were not previously known from the Yukon. About half of the Yukon Heteroptera and of the Cicadellidae are recorded for the first time by Scudder (1997*b*) and Hamilton (1997). Such lists also include new Canadian and North American records. Some of the additions result from careful examination of museum specimens; others stem from deliberate programmes of active collecting (e.g. Scudder 1997*b*; Wiggins and Parker 1997). In groups where taxonomy and collecting are adequate, expert prediction of total expected Yukon species has been possible (see Table 1 below).

Fossil evidence is available for carabid beetles (Ball and Currie 1997) and for some other taxa (Matthews and Telka 1997). Numerous exposures of fossil-bearing sediments in the Yukon Territory make this information particularly plentiful, allowing intersecting evidence about the fauna to be compared, and so avoiding the need to rely on a single type of evidence in drawing biogeographical conclusions.

A great advantage of the data brought together here is the range of taxa investigated, including representatives of more than 150 families in all of the major orders of insects. Although information for many of the beetle families is based chiefly on a recent checklist rather than on the more comprehensive treatment of Yukon species available for Carabidae, Dytiscidae, and Curculionidae, the Coleoptera is the best known order of insects (Arnett 1990).

Taxa treated here vary widely in the state of knowledge, but some are quite well known (e.g. Odonata, Heteroptera, Carabidae, Dytiscidae, butterflies), and taxa vary too in other attributes. Both terrestrial and aquatic taxa are treated, and they include a wide range of feeding types: for example, some groups are primarily or exclusively predators (e.g. Odonata, Sphecidae); others are herbivores (e.g. Lepidoptera, Cicadellidae).

Several ecologically very important groups are included. Oribatid mites are dominant soil forms, largely replacing earthworms and other large invertebrates in northern life zones, at least in moister and richer soils (Behan-Pelletier 1997). Dytiscids are the dominant group of northern aquatic beetles (Larson 1997). Sphaerocerid flies are ubiquitous and abundant in various substrates (Marshall 1997). And weevils, though not well represented in the Yukon, belong to the largest family of beetles and are characterized by an especially great diversity of relationships with plants.

In addition to very diverse groups are a number of taxa that are less diverse (e.g. Ephemeroptera), or less diverse in the Yukon (e.g. Orthoptera). Finally, data on taxa of primarily

northern affinities (Dytiscidae, Chironomidae) as well as on primarily southern groups (Orthoptera, Odonata) are available for comparison.

In summary, the diversity of taxa for which data are available—despite caveats given in the next section—suggests that these taxa will prove adequate to identify the important features of the Yukon fauna.

Weaknesses of the Data. Before treating the data in more detail, some caveats are offered about particular data sets, because the amount of taxonomic work, collecting and other studies varies widely among the taxa and it has not been possible to study every group. Of course, although taxa covered are believed to be adequately representative as just noted, and they reflect a large proportion of what is currently feasible, a potential initial weakness is the fact that only half of the known species likely to be present in the Yukon are in the groups treated in preceding chapters; in the absence of potential authors or of sufficient taxonomic information, there is no treatment of some important groups of Hymenoptera (notably the sawflies, and parasitoids like the ichneumonids), nor of several characteristic families of Diptera (such as tipulids, mycetophilids and muscids). The data on most families of beetles is derived from less specific study of Yukon material than for the other taxa treated here.

In some taxa, taxonomic knowledge is inadequate for North American species, so that it is difficult to put the Yukon fauna into perspective (e.g. Cannings 1997 for Asilidae). Oribatid mites are relatively little known in North America; perhaps only a quarter of the species have been described (Behan-Pelletier 1997). In some groups, it has nevertheless been possible to recognize specific entities even though they are not yet formally described. In the Formicidae, considerable taxonomic difficulties are created by the existence of similar and variable species and by the fact that only small samples, typically without the reproductive morphs, are available for many species (Francoeur 1997). Even in some better known groups the status of fossil species, especially more ancient ones, is uncertain (Matthews and Telka 1997).

A second major problem is the fact that collecting is deficient or distorted. When ranges are inadequately known, conclusions must be tentative (e.g. Wilson 1997). Particular problems are created in some groups by limitations of data from the Palaearctic region (cf. Currie 1997), leading to the likelihood of additional synonymies when more material of some species, which will prove to be Holarctic, is available from Eurasia. Data from the Russian Far East is especially deficient for some taxa. Indeed, Griffiths (1997) believes that species apparently disjunct between the Yukon and Europe also occur in northern Asia but have not yet been collected there. Even in the Nearctic region, collecting is deficient in some taxa. Aphid species known only from Beringia almost certainly reflect merely inadequate sampling or taxonomic problems (Footit and Maw 1997). Marshall (1997) supposed that peatland species of sphaerocerids with Yukon-eastern Nearctic disjunct ranges occur in central Canadian peatlands but these habitats have not yet been adequately sampled. As a result, the recorded “ranges” of species that have rarely been collected change when more records become available.

At a smaller scale, records of distributions within the Yukon Territory vary widely in completeness. Some records reflect the role of access provided by highways, lakes and navigable rivers more than actual ranges (e.g. Currie 1997; Vickery 1997). Also, the completeness of samples depends on the number and nature of specimens collected, according to the techniques used, the amount of effort spent, and—in groups for which special knowledge or techniques are required—the availability of expertise. Collecting nevertheless appears to be especially deficient or biased in only a few groups. Relatively

few aphids have been collected, from relatively few sites (Footitt and Maw 1997). Chironomids from only 3 sites on the arctic slope have been investigated (Oliver and Dillon 1997): the known distribution of species such as *Lipurometriocnemus vixlobatus* Sæther (so far collected only in the Yukon Territory and in South Carolina) is clearly incomplete. Relatively few sites have been collected for mayflies, which tend to be difficult to acquire and preserve by general collecting. Harper and Harper (1997) suspect that the relatively small numbers of mayfly species known from the Yukon may result from incomplete collecting.

On the other hand, oribatid mites and sphaerocerid flies may be over-represented in Yukon samples compared to collections from the rest of North America (where they are inadequately known anyway), because these northern forms have received some specific attention in the Yukon that was not brought to bear elsewhere (Behan-Pelletier 1997; Marshall 1997).

In other groups, the adequacy of collecting varies among different habitats. For example, Hamilton (1997) suggests that leafhopper collections are likely to be biased toward boreal species, which inhabit the forested river valleys where most roads are situated. Conversely, Lafontaine and Wood (1997) conclude that boreal species of Lepidoptera are under-represented in collections, because many collectors merely pass through boreal sites on their way to study more distinctive arctic and alpine areas. Chironomids from large water bodies have not been collected (Oliver and Dillon 1997).

The difficulty of access also means that collections may not have been made throughout the season. Currie (1997) concluded that early spring-emerging species of black flies are under-represented in Yukon collections.

Ancillary data are deficient for many species. For some collections, and for typical museum specimens, habitat information is rarely available (Griffiths 1997), especially on a relatively fine scale (Ball and Currie 1997). Finally, although most species recorded from the Yukon probably are truly resident (i.e. breeding) there, evidence from some better known groups suggests that a few species may instead be migrants (compare the maps of resident and migrant areas of North American butterflies: Scott 1986), adults flying strongly into areas in which they do not breed (some dragonflies: Cannings and Cannings 1997), or even species "blown in" (compare the leafhopper *Psammotettix latipex* (DeLong and Davidson): Hamilton 1997).

Therefore, groups in which collecting and taxonomic work have been insufficient provide little clear evidence of faunal development. Moreover, even detailed data may be equivocal if they are not complete in time and space. Vickery (1997) pointed out that available taxonomic and distributional evidence for grasshopper species of the genus *Melanoplus* is not sufficient to tell whether they survived the Pleistocene in the Yukon or in a southern refugium. These caveats do not affect the great value of the data as explained at the beginning of this section, but they indicate which few taxa might be excluded from some subsequent analyses to avoid bias (as footnoted in Table 1 below). The remaining groups have more reliable data.

Taxonomic Patterns

The current fauna reflects the interplay of phylogenetic history, and hence existing adaptations of the taxa, with current environments and their history. The biological species is the level at which these processes can be analyzed: typically, species are the functioning entities in nature, and they are the means by which all biological information is organized and retrieved, as pointed out by Danks (1988). Species thus are currently the only fully

cataloguable entities. Each species brings for study a unique history and a unique evolution and set of adaptations. Unfortunately, details of these properties, and even of basic current ecological requirements, are not available for most of the Yukon species. Nevertheless, simple statistics about the occurrence of sets of individual species provide surprisingly useful insights into faunal ecology and evolution. This section on taxonomic patterns summarizes basic information on the number of species in the Yukon, the composition of its fauna compared to elsewhere, and some features of differentiation and variation. The further meaning of the trends revealed is explored in the final section of this paper when data on ecology and distribution have also been summarized.

Number of Species and North American Comparisons. The numbers of species, grouped in families and orders, recorded from the Yukon by authors in this volume are shown in the second column of Table 1. When the total numbers of species in the Yukon were estimated by authors, these are shown in the next column. Such extrapolations are possible in better known groups especially from information from other temperate areas and from the relative representation of better known and less well known subgroups (cf. Lafontaine and Wood 1997). The 2 subsequent columns of the table show the numbers of species recorded from Canada, and the numbers recorded from North America as a whole, based on sources cited in Table footnotes.

For arachnids, 297 species of spiders in 17 families and 157 species of oribatid mites in 50 families are recorded here from the Yukon. For insects, some 2711 species in 156 families are recorded. The families treated in earlier chapters include about one third of the known arachnid fauna, and more than half of the known insect fauna, of Canada and of North America—compare Danks (1979), Kosztarab and Schaefer (1990) and other references cited in table footnotes. Although some important groups have not been treated, many characteristic families have; extrapolating the current data on the basis of knowledge for Canada as a whole suggests that the total Yukon fauna comprises about 900 arachnid species and nearly 6000 insect species, with many additional species still undiscovered or undescribed.

The table (final line) shows that the number of species recorded from Canada that have been recorded in the Yukon is about 20% for insect groups with more reliable data that are treated in detail in this book. The percentage falls to only 16% if the many other families of Coleoptera, treated here in less detail, are included (preceding line of the table); however, the Coleoptera is the most southern of the major orders, and comparable data for the dominant northern Diptera and Hymenoptera are not available. The mean percentage for Yukon species of spiders is 22% of the fauna of Canada. These reductions in diversity reflect 2 main factors. First, the Yukon is much smaller than Canada as a whole (about 5% of the area). However, many Canadian species are widespread: more than a third of species occur both east and west of Manitoba, and the provinces of British Columbia and of Ontario each contains well over half of the country's known fauna (Danks 1993). Consequently, much of the low Yukon diversity can be attributed instead to the relatively severe climatic and ecological conditions in this predominantly subarctic and boreal region (see Introduction above; Scudder 1997*a*), which would be inhabited chiefly by species adapted to such environments.

The percentage of Canadian species in the Yukon varies widely from group to group. In particular, many Canadian families, especially less diverse families, are not listed in the table because they are not represented in the Yukon Territory. For spiders, 18 families that occur in Canada do not occur in the Yukon (Table 1; Danks 1979), one half of the number of Canadian families. For only those insect groups reported on in their entirety in this book

TABLE 1. The numbers of species in the Yukon and elsewhere—grouped in families and orders—for taxa treated in this book. Numbers of families in each order that occur in the different regions are shown in brackets []. Data for “other families” in Canada show both the number of species for all of those other families, and the number of species (marked Y) for only those families that occur in the Yukon. For sources of data, see footnotes.

Taxon	No. recorded Yukon spp. ¹	Est. total Yukon spp. ²	No. recorded Canadian spp. ³	No. recorded North American spp. ⁴	Yukon spp. as percent of Canadian spp.	Canadian spp. as percent of North American spp.	State of collecting in the Yukon ⁵
ARACHNIDA							
Araneae	297 [17]	336+	1377 [35]	3762 [57]	22	37	
Araneidae	16		61	192	26	32	
Dictynidae	10		60	159	17	38	
Erigonidae	102		309	591	33	52	
Gnaphosidae	23		100	330	23	30	
Linyphiidae	34		136	254	25	54	
Lycosidae	30		107	300	28	36	
Philodromidae	13		47	102	28	46	
Salticidae	17		100	288	17	28	
Theridiidae	14		93	231	15	40	
Thomisidae	17		63	121	27	52	
Other families	21		301 (259Y)	1194	7	25	
Oribatida	157 [50]	393	385+ [73]	908 [120]	41-	39+	+
INSECTA							
	? [?]		29 976	90 251	?	33	
Ephemeroptera	30 [8]	50+	296 [15]	672 [16]	10	44	-
Ameletidae	1		16	33	6	48	-
Baetidae	7		71	143	10	50	-
Ephemerellidae	4		44	108	9	41	-
Heptageniidae	8		73	137	11	53	-
Leptophlebiidae	2+		24	79	8+	30	-
Siphonuridae	5		16	26	31	62	-
Other families	3		52 (13Y)	127	6	41	-
Odonata	33 [5]		202 [10]	437 [12]	16	46	=
Aeshnidae	9		24	37	38	65	=
Coenagrionidae	4		42	98	10	43	=
Corduliidae	10		29	49	34	59	=
Libellulidae	8		45	105	18	43	=
Other families	2		62 (9Y)	147	3	42	=
Plecoptera	71 [8]		250 [9]	608 [9]	28	42	
Capniidae	18		49	129	37	38	
Chloroperlidae	18		44	59+	41	75-	
Leuctridae	5		21	45	24	47	
Nemouridae	12		32	61	37	52	
Perlodidae	12		61	97+	20	63-	
Other families	6		43 (39Y)	206+	14	21-	
Orthoptera	17 [2]		214 [8]	1804 [11]	8	12	
Acrididae	14		124	600	11	21	
Other families	3		90 (7Y)	1204	3	7	
Heteroptera	216 [19]		1265 [38]	3836 [47]	17	33	=
Anthracoridae	14		35	75	40	47	=
Aradidae	11		52	123	21	42	=
Corixidae	11		71	125	15	57	=
Lygaeidae	19		117	318	16	37	=
Miridae	112		650	1930	17	34	=
Pentatomidae	6		69	222	9	31	=
Saldidae	17		37	69	46	54	=
Tingidae	4		36	154	11	23	=
Other families	22		198 (117Y)	819	11	24	=

TABLE 1. (continued)

Taxon	No. recorded Yukon spp. ¹	Est. total Yukon spp. ²	No. recorded Canadian spp. ³	No. recorded North American spp. ⁴	Yukon spp. as percent of Canadian spp.	Canadian spp. as percent of North American spp.	State of collecting in the Yukon ⁵
Homoptera	? [?]		1901 [29]	6970 [38]	?	27	
Aphidoidea	53	108	650	1400	8?	46	–
Cicadellidae	145	166	800	2800	18	29	
Delphacidae	30		81	303	37	27	–
Coleoptera	913 [57]		7436 [112]	23 824 [125]	12	31	
Anobiidae	5		79	299	6	26	
Buprestidae	13		152	675	9	16	
Cantharidae	8		126	468	6	27	
Carabidae	209		946	2271	22	42	=
Cerambycidae	27		354	956	8	37	
Chrysomelidae	41		569	1481	7	38	
Cicindelidae	4		46	108	9	43	=
Coccinellidae	31		162	399	19	41	
Cryptophagidae	1		66	152	2	43	
Curculionidae	59		609	2614	10	23	
Dytiscidae	113	135	262	475	43	55	=
Elateridae	32		369	885	9	42	
Histeridae	2		118	499	2	24	
Hydrophilidae	20		149	284	13	52	
Leiodidae	28		128	321	22	40	
Mordellidae	1		70	207	1	34	
Nitidulidae	10		101	183	10	55	
Scarabaeidae	10		248	1395	4	18	
Scolytidae	33		204	480	16	42	
Staphylinidae	179		1129	3187	16	35	
Tenebrionidae	3		135	1008	2	13	
Other families	84		1414 (1039Y)	5477	6	26	
Families with more detailed info. (Carabidae, Dytiscidae, Curculionidae)	(381)		(1817)	(5360)	(21)	(34)	
Diptera	? [?]		7058 [101]	19 562 [121]	?	36	
Anthomyiidae (part)	131	151	296	403	44	73	
Asilidae	20	35	125	1011	16	12	
Chironomidae (part)	103	300+	480?	953?	21?	50?	–
Simuliidae	55	76	160	265	34	60	
Sphaeroceridae	59	74	35+	199	?	?	+
Lepidoptera	518 [24]	2000	4692 [68]	11 283 [72]	11	42	
Gelechiidae	11		525	630	2	83	–
Pyrilidae	38		400	1374	9	29	–
Tortricidae	60		510	1054	12	48	–
Other Microlepidoptera (Microlepidoptera)	27 (136)	(1200)	748 (403 Y) (2183)	2347 (5405)	4 (6)	32 (40)	–
Hesperiidae	6		64	290	9	22	=
Papilionidae	5		18	33	28	55	=
Pieridae	16		37	63	43	59	=
Lycaenidae	13		59	161	22	37	=
Nymphalidae (Butterflies/skippers)	48 (88)	(90)	93 (271)	210 (760)	52 (32)	44 (36)	=
Arctiidae	19		70	264	27	27	
Geometridae	95	250	450	1404	21	32	
Noctuidae	168	400	1520	2925	11	52	

TABLE 1. (continued)

Taxon	No. recorded Yukon spp. ¹	Est. total Yukon spp. ²	No. recorded Canadian spp. ³	No. recorded North American spp. ⁴	Yukon spp. as percent of Canadian spp.	Canadian spp. as percent of North American spp.	State of collecting in the Yukon ⁵
Notodontidae	3		50	136	6	37	
Sphingidae	5		54	124	9	44	
Other							
Macrolepidoptera	4		94 (26Y)	265	4	35	
(Macrolepidoptera excl. butterflies/skippers/Noctuidae/Geometridae)	(31)	(60)	(268)	(789)	(12)	(34)	
Trichoptera	145 [15]		571 [22]	1305 [26]	25	44	
Glossosomatidae	3		24	76	12	32	
Hydropsychidae	10		46	147	22	31	
Hydroptilidae	5		71	227	7	31	
Lepidostomatidae	6		29	66	21	44	
Leptoceridae	16		59	109	27	54	
Limnephilidae	57		139	227	41	61	
Phryganeidae	13		26	28	50	93	
Polycentropodidae	6		35	69	17	51	
Rhyacophilidae	14		58	118	24	49	
Other families	15		84 (69Y)	238	18	35	
Hymenoptera	? [?]		6028 [75]	17 429 [81]	?	35	
Chrysoidea	31		150	474	21	32	
Sphecidae	70		283	1139	25	25	
Vespoidea (excl. ants)	52		316	1381	16	23	
(Aculeate wasps excl. Formicidae)	(153)	(187)	(649) (583Y)	(2994)	(24)	(22)	
Formicidae	19	25	139	560	14	25	–
Total Insecta, only groups with Yukon data, as listed above	2711		18 341	54 656	15	33	
Total Insecta, groups with Yukon data but excluding less reliable data (– or + in final column)	2283		14 477	45 164	16	32	
Total Insecta, groups treated in detail (hence excluding many Coleoptera), and excluding less reliable data	1751		8858	26 700	20	33	

¹ According to authors in this volume.² According to authors in this volume.³ Various sources, including authors in this volume, D.R. Paulson and S.W. Dunkle for Dragonfly Society of the Americas (Internet), and pers. comm. from V.M. Behan-Pelletier, S.G. Cannings, D.C. Currie, C.D. Dondale, P.P. Harper, S.B. Peck and G.B. Wiggins; otherwise from Danks (1979), Bousquet (1991).⁴ As for ³ above, including Hodges et al. (1983), McCafferty (1996), Scudder (1997b), or according to Kosztarab and Schaefer (1990), Danks (in press)[some totals], Merritt and Cummings (1989), or Arnett (1990). Some additional minor updates would be feasible for many taxa, but would not change the results appreciably.⁵ –, less well collected in the Yukon than elsewhere, or not well collected; +, probably better collected in the Yukon than elsewhere; =, relatively well collected everywhere. For details see text section on The Information Available.

(and hence without appropriate data for the major orders Homoptera, Diptera and Hymenoptera as well as other smaller orders), 144 Canadian families of insects (Table 1; Danks 1979) have not been reported from the Yukon, again about half of the total number of Canadian families in the groups treated. In contrast, some other families have half or even more of their Canadian species in the Yukon. The relative representation of these families is discussed below under Composition of the Fauna.

The penultimate column of the table shows the percentage of North American species in Canada for each group, 32–33% for all Canadian species (Table 1, "Insecta") as well as for the data from the Yukon (Table 1, last 3 lines). Groups with relatively high percentages of North American species in Canada as shown in this column can be considered as more or less "northern", or at least they comprise chiefly widespread species tolerating northern as well as southern conditions. Groups with relatively low percentages include chiefly species of southern affinities or generally restricted distributions (and compare Danks 1994a). The final column of the table suggests the state of collecting for selected families. Further details about groups considered here to be undercollected in the Yukon (–), or more fully collected there relative to elsewhere (+), were given above in the section The Information Available. Such groups, for which the data are likely to be less reliable, comprise about one sixth of the species. These taxa are excluded for most subsequent numerical analyses, though not for the purpose of more general discussion.

Several families (marked = in the table) have been much better collected in both the Yukon and Canada than have most other groups. Dragonflies and butterflies are large and conspicuous, very well known taxonomically, and with many interested students. The Heteroptera have been the subject of intensive study and collecting in Canada and the Yukon by G.G.E. Scudder. The ground beetles (Carabidae) and predaceous water beetles (Dytiscidae) have been studied by many entomologists in Canada.

Comparison with Adjacent Areas. Reliable comparison of the number of species in the Yukon with adjacent areas is difficult for most groups because records for Alaska and the adjacent Northwest Territories are deficient. In general, numbers of species known for Alaska (area 1 501 200 km²) are about the same as or slightly more than for the Yukon Territory (482 000 km²) in better collected groups (e.g. Araneae, Orthoptera, Cicadellidae, Carabidae, Curculionidae, Trichoptera), but fewer species have been recorded, of course, when a group has been less well collected in Alaska (e.g. Heteroptera, Dytiscidae). For beetles as a whole, which have been relatively well collected in northern North America, 913 species are known from the Yukon, 1205 from Alaska, and 1031 from the Northwest Territories (Anderson 1997a). At least in groups with many widely distributed species, the Yukon and Alaskan faunas overlap widely. Twenty-two of 33 Yukon dragonflies have been recorded from Alaska, and another 9 are expected (Cannings and Cannings 1997, table 1). Known from Alaska are 684 of the 913 Yukon species of Coleoptera (from data in Anderson 1997a). In asilids and mayflies, fewer than half the species so far known are in common, but these groups are not at all well collected. Data on the number of species are generally too scanty for reliable comparison between the Yukon and the Northwest Territories, although 641 of the 913 species of Yukon beetles are included in the 1031 species known from the Northwest Territories (from data in Anderson 1997a).

As might be expected, British Columbia to the south has many more species than the Yukon: up to twice as many in groups with widely distributed northern species (e.g. 168 vs. 113 in Dytiscidae, 279 vs. 145 in Trichoptera). In some more southern groups, more than 3 times as many species occur in British Columbia compared to the Yukon (e.g. 640 vs. 216

in Heteroptera), and more than twice as many even in the widely ranging and widely distributed Odonata (72 vs. 33).

Such differences partly reflect differences in the extent of arctic, boreal and other zones in the Yukon and adjacent areas, but limitations of data, especially for Alaska and the Northwest Territories, hinder comparisons. Nevertheless, the overlap in species between some of these adjacent northwestern areas appears to be smaller than might be expected.

Data in many preceding chapters show that the numbers of species in different regions within the Yukon approximately follow the regional severity of climate. Thus, many species are confined to the south, and many other species drop out toward the north until fewest species occur on the arctic coastal plain, although a few "arctic" species are added there (e.g. Cannings and Cannings 1997, table 2; Hamilton 1997, table 2; Wiggins and Parker 1997, table 1). The attenuation is particularly marked in groups of southern affinity, such as aculeate wasps and Orthoptera. However, it is slowed by the interdigitation of relatively favourable habitats far to the north (see Introduction). These general trends reflect the geographic and zonal ranges of particular species.

Composition of the Fauna. Because taxa are differentially represented in the Yukon as compared to elsewhere, the fauna has a characteristic composition. Some groups decline markedly from south to north, at specific, generic and ordinal levels, and make up a decreasing proportion of the fauna. Relative to more temperate regions, there are few Yukon species of dragonflies, weevils, asilids and ants, for example. The hydropsychid caddisflies, a dominant group elsewhere, are not well represented (Wiggins and Parker 1997). Most families of the order Heteroptera are not well represented in the north, and the order as a whole (17% of Canadian species), and individual families such as Tingidae and Pentatomidae, are not well represented in the Yukon.

Conversely, some other groups are more diverse than might be expected, such as dytiscids and leafhoppers. Therefore, certain taxa and subtaxa dominate the faunal composition. For example, half of the Yukon oribatid mites belong to only 6 of the 50 families recorded there (Behan-Pelletier 1997). Nearly half of the North American species of Colymbetinae (a dytiscid subfamily characteristic of colder regions) occur in the Yukon (Larson 1997). Most Yukon caddisflies are in the generally northern family Limnephilidae and in other northern genera such as *Agrypnia* (Phryganeidae) (Wiggins and Parker 1997). Yukon carabids belong chiefly to northern subgroups (Ball and Currie 1997), such as *Pterostichus* (*Cryobius*).

Insects and spiders best and least well represented at the family level in the Yukon (based on the Yukon/Canada percentage in Table 1) are listed in Tables 2 and 3. These families are considered in more detail in a later section in seeking possible explanations for faunal composition (see Ecological Correlations).

Families best represented in Canada relative to North America as a whole, and hence more northern (or at least widespread), tend also to be best represented in the Yukon relative to Canada as a whole (Table 4). In other words, as might be expected from the nature of Yukon environments, northern groups dominate the Yukon fauna.

The composition of the fauna appears to reflect existing properties of taxa, or adaptations of groups that favour their survival under the environmental conditions of the Yukon. Thus both taxonomic relatedness of species, and the "northernness" of a family, subfamily or genus, tend to be correlated with Yukon occurrence. The same correlation exists for arctic insects (Danks 1981). Fossil evidence suggests that most insect species respond to environmental change by movement rather than by rapid change in properties (Matthews 1979;

TABLE 2. Some insect families best and least well represented in the Yukon (from Table 1).

Family	Percentage of Canadian spp. in Yukon
Nymphalidae	52
Phryganeidae	50
Saldidae	46
Anthomyiidae	44
Dytiscidae	43
Pieridae	43
Chloroperlidae	41
Limnephilidae	41
Anthocoridae	40
Aeshnidae	38
Capniidae	37
Nemouridae	37
Corduliidae	34
Simuliidae	34
Arctiidae	27
Leptoceridae	27
Carabidae	25
Sphecidae	25
Leuctridae	24
Rhyacophilidae	24
Mean for all species in groups treated in detail in this book that have reliable data	20
Asilidae	16
Lygaeidae	16
Vespoidea	16
Corixidae	15
Glossosomatidae	12
Acrididae	11
Noctuidae	11
Tingidae	11
Coenagrionidae	10
Curculionidae	10
Hesperiidae	9
Pentatomidae	9
Sphingidae	9
Hydroptilidae	7
Notodontidae	6
Many other, especially smaller, families	0

TABLE 3. Some spider families best and least well represented in the Yukon (from Table 1).

Family	Percentage of Canadian spp. in Yukon
Erigonidae	33
Lycosidae	28
Philodromidae	28
Thomisidae	27
Araneidae	26
Linyphiidae	25
Mean for all species	22
Dictynidae	17
Salticidae	17
Theridiidae	15
Many other, especially smaller, families	0

TABLE 4. Number of insect families in the Yukon compared to Canada, in relation to Canada compared to North America (for families with available reliable data in Table 1).

Representation in Yukon compared to Canada	Representation in Canada compared to North America	
	Well represented (more than 50% of N. Am. spp.)	Less well represented (less than 50% of N. Am. spp.)
Very well represented (more than 30% of Canadian spp.)	10	3
Less well represented (less than 20% of Canadian spp.)	4	31

Danks 1981; Elias 1994). Yukon species as far as is known likewise follow previous preferences or habitats (e.g. riparian species and fungivorous species of sphaerocerids: Marshall 1997), and the pre-existing habits of genera, not new sets of tolerances, predict the occurrence of stoneflies (cf. Stewart and Ricker 1997 for cold stream/mountain species). Ecological or historical explanations for the nature of the Yukon fauna can start from such a taxonomic foundation.

Variation. Intraspecific variation and differentiation in Yukon species are useful in tracing the history of the fauna. As Wiggins and Parker (1997) point out, patterns of variation usually are assumed to be genetic, in the absence of evidence to the contrary, and thus allow strong biogeographic inferences. Information on genetic variation is available on relatively few Yukon species, and many taxonomic problems remain as noted in earlier chapters, but species show one of at least 3 different patterns. First, Yukon populations of many widespread species show no differentiation from populations elsewhere (e.g. weevils: Anderson 1997b). Second, species are variable, but few or no congruent or coherent geographical trends are recognizable (e.g. Wiggins and Parker 1997 for the caddisfly *Onocosmoecus unicolor* (Banks)), although many such conclusions are based on limited information.

Third, species in the Yukon Territory and elsewhere differ at the population or subspecific level. The data allow few generalizations—for example, one cannot assert that northern or Yukon forms are more or less variable as such than southern ones, because even within a particular group (for example Carabidae: G.E. Ball, pers. comm.) the extent of variation depends mainly on the subgroup. Nevertheless, the Yukon information shows several kinds of differences that merit more detailed investigation: in taxonomic characters (e.g. the caddisfly *Agrypnia colorata* Hagen: Wiggins and Parker 1997); in size (e.g. the smaller Yukon specimens of the dragonfly *Sympetrum internum* Montgomery: Cannings and Cannings 1997); and in the extent of the variation, such that relict montane populations are more variable in genitalic structure than northern North American populations (*Agrypnia glacialis* Hagen: Wiggins and Parker 1997). Differences in colour—or the brightness of colour—and in wing development or structure between arctic and temperate populations of some Lepidoptera and Diptera provide another point of departure (e.g. Downes 1962, 1964, 1970).

Wing Loss and Other Structural Modifications. Species in several Yukon taxa show wing reduction or loss. This character is especially interesting because it may be correlated with isolation, and therefore may pertain to survival or evolution in Beringia.

However, wing loss is not correlated *simply* with anything (Darlington 1943), but has been associated, depending on the taxon, with the effects of low temperature (especially

when it is too cold to fly), habitats (e.g. those where running rather than flying is effective and especially those that are persistent), energy conservation (e.g. for oviposition; and also wings may be lost to save energy if merely neutral) and compensation for disadvantageous dispersal by wind (review by Danks 1981, p. 269; Roff 1990).

Among Yukon species of Lepidoptera, some females are brachypterous and cannot fly (e.g. *Acsala anomala* Benjamin), some have larger wings than males but apparently do not fly (*Gynaephora* spp.) and some have smaller wings than males and fly less frequently (e.g. *Xestia tecta* (Hübner)) (Lafontaine and Wood 1997). Downes (1964, plate II) and Lafontaine and Wood (1997, frontispiece, lower right) illustrate this type of wing reduction in northern moths. Brachypterous insects from the Yukon also include species of antho-corids, delphacids, leafhoppers, weevils, carabids, and sphaerocerids. Some of them show a range of wing loss, or at least long- and short-winged morphs within the species, as for the sphaerocerid *Aptilotus luctuosus* (Spuler), and 32 species of Yukon carabids (Ball and Currie 1997). Two subgroups of brachypterous carabids in the genus *Pterostichus* are especially well represented in the Yukon fauna.

Many brachypterous species belong to taxa that are brachypterous elsewhere, and so wing loss is simply a phylogenetic rather than regional character. Several species of moths are in this category (Lafontaine and Wood 1997). Six of the 10 wingless species of Yukon weevils are Beringian, but again most of them are in groups where wing loss is widespread (Anderson 1997b).

Many species with wing reduction belong to groups associated with particular habitats. Brachypterous Delphacidae are characteristic of stable habitats (Wilson 1997). Most tundra carabids in the Yukon territory have reduced wings, compared with about 50% in forest or general habitats, and few in riparian habitats (Ball and Currie 1997). Brachypterous leafhoppers are common in the Yukon, but are associated not with latitude or isolation, but with low-growing plants such as grasses that are dominant or subdominant, making it easy for individuals to reach new food sources (Hamilton 1997).

Nevertheless, a few very interesting wingless or brachypterous species are members of groups where wing reduction is not typical. They include 6 Beringian Lepidoptera (Lafontaine and Wood 1997), and the Beringian weevil *Ceuthorhynchus barkalovi* Korotyaev (Anderson 1997b). Moreover, brachyptery is much more common in carabids with Beringian ranges (68% of Beringian species) than in more widely distributed species, in which macroptery or wing dimorphism predominates (Ball and Currie 1997). Although there are relatively few examples, secondary wing reduction in species with restricted ranges suggests the role of Beringian history in wing reduction in these instances.

A second noteworthy set of modifications occurs in chironomid midges in Beringia and adjacent areas, consisting of reduced antennae, a swollen hypopygium, often female-dominated sex ratios, and other characters listed by Oliver and Dillon (1997). These modifications are associated chiefly with loss of aerial mating in severe habitats such as the arctic, and elsewhere are associated with small discrete habitats such as rock pools and springs (references cited by Oliver and Dillon 1997).

Severe or arctic conditions and isolation therefore are correlated with both wing reduction and other structural modifications in a small but significant number of Yukon species. Such environments were present in Beringia during the Pleistocene (e.g. Schweger 1997).

Ecological Patterns

The nature of the fauna reflects the ecological requirements of each species. Data on most individual species from the Yukon are relatively limited, but nonetheless some general

ecological features can be detected from detailed information on some species and from the fact that broad ecological requirements often can be predicted from the characteristics of related species. Some general relationships of Yukon insects with habitats, with food and with other organisms, and some aspects of adaptation, are first outlined. The last subsection correlates these features with the representation of certain taxa in the Yukon.

Habitats. Habitats for insects in the Yukon tend to be warmer for their latitude than elsewhere in Canada (see Introduction). Partly as a result of this, the Yukon contains a very wide variety of both terrestrial and aquatic habitats for insects. Habitats of low arctic, subarctic, boreal and transition zones are represented, ranging from cold tundra to relatively rich forests and sun-warmed slopes. Some of these zones, especially the boreal forest, are very extensive. In addition, the terrain is topographically complex, especially the Cordillera, with many mountain ridges and many valleys and their streams.

Terrestrial habitats vary chiefly in extent, type of vegetation, temperature, insolation, and water relationships, which are inter-related and in turn depend on slope, aspect, soil type and other factors. Habitat diversity in arctic and alpine terrain is reduced by the lack of trees, and by the fact that especially in the northern Yukon the full soil profile is not available to organisms because of permafrost (e.g. Behan-Pelletier 1997). Large forested areas are cold muskeg. Nevertheless, though habitats are predominantly cold and seasonal, the heterogeneity of natural habitats is relatively high, and each area offers a mosaic of conditions. For example, locally favourable, moister, warmer, completely vegetated areas are available even in relatively severe arctic regions (review by Danks 1981). Forest diversity is greatly increased by the effects of fire and subsequent regeneration of stands of various ages (e.g. Douglas 1974; Danks and Footit 1989; Oswald and Brown 1990). Open areas in the forest offer relatively warm and sunny conditions. Heterogeneity is increased further by the diversity of microhabitats, with fine-scale differences, for example in temperature, moisture and food availability including hostplant species.

River valleys and their adjacent slopes provide a number of relatively favourable habitats, though they tend to be progressively restricted or interrupted northward. At a larger scale, these valleys permit trees to extend toward the north. On a smaller scale, the south-facing slopes make available important sun-warmed grass-sage and similar habitats, often referred to as "xeric grassland", "steppe" or "southern steppe" (e.g. Lafontaine and Wood 1988, 1997; Hamilton 1997; Scudder 1997b). At a still smaller scale, local outliers such as warm, well-drained gravel banks or bars along rivers can support a vegetation and fauna of quite southern aspect, even as far north as 67°N. By the same token, cold habitats extend into southern zones. The dytiscid beetle *Agabus clavicornis* Sharp occurs southward into British Columbia in spring-fed pools on north-facing slopes (D.J. Larson, pers. obs.).

Most groups of Yukon insects contain species with many different habitats, using many different resources (see Trophic relationships below). For example, different species of weevils in the Yukon occupy wetlands or forests, and feed on roots, stems, reproductive structures, leaves or aquatic plants (Anderson 1997b). Some carabid beetles, including 3 species of *Sericoda*, are associated with burned forest (Ball and Currie 1997). Terrestrial, as well as fully aquatic, chironomids are well represented in the North Slope fauna (Oliver and Dillon 1997).

When the data are good enough, characteristic habitat associations can be recognized for the species (e.g. Ball and Currie 1997), though of course specific habitats cannot be inferred from broad information about the ranges or life zones of the species. Indeed, treeline as such (the boundary between major zones for many terrestrial organisms) appears to have

little effect on leafhoppers, which feed on sedges and grasses (Hamilton 1997). Habitat features differ in importance among groups. For example, the distinction between wet tundra and dry tundra species is an important one for Lepidoptera (Lafontaine and Wood 1997), but carabid beetles are not distinguished on this basis, even though riparian and xerophilous species can nonetheless be recognized farther south (Ball and Currie 1997). Again, many carabids occupy the litter layer, so that the composition of tundra plants or the structure of a shrub or tree layer is less important to them than to truly plant-associated groups. In some groups, foodplant and habitat elements are combined. For example, most delphacids occur on grasses and sedges in wet habitats (Wilson 1997). Finally, several terrestrial species from the Yukon, such as those associated with mammal runs and burrows (e.g. anthomyiids of the genus *Eutrichota*: Griffiths 1997; sphaerocerids such as *Spelobia lispina* Marshall and *Crumomyia subaptera* (Malloch): Marshall 1997), have very specific habitats that are not based on foodplant relationships.

Warm, sunny, open areas, such as breaks in the forest, are important for warm-adapted groups. Such sites are used for hunting by asilids, for example (Cannings 1997). The existence and northward occurrence of species in several groups are linked with milder river valleys and associated sun-warmed slopes, as for aculeate wasps, leafhoppers, and characteristic heteropterans (Finnamore 1997; Hamilton 1997; Scudder 1997b).

Aquatic habitats are numerous and diverse in the Yukon. They vary widely in temperature, permanence and other features, as influenced especially by size, water supply, flow rate, seasonality (including the extent of freezing), nutrient or resource availability, substrate type, exposure, vegetation, and type of surrounding vegetation (see also Danks 1981; Danks and Williams 1991; Cannings and Cannings 1997; Larson 1997; Wiggins and Parker 1997). These interacting factors produce aquatic habitats that can be classified in various ways, but consist of several main types. Large lakes are cool and relatively stable. Small lakes and ponds are warmer in summer but frozen solid in winter except for some spring-fed pools; locally some are alkaline. Shallow pools produced by thermokarst processes are very numerous on the coastal plain. Very shallow habitats include transient pools and seepage areas. Potentially more complex lentic habitats common in the Yukon include bogs, shallow sedge/moss fens and relatively nutrient-rich sedge marshes. There are especially large numbers of shallow lentic habitats, many of which are relatively rich in detritus or other organic materials.

Lotic habitats include large relatively cool rivers of considerable flow (but differing widely in gradient), slow relatively warm streams, and rapid cool mountain streams. Springs are especially cool and stable, and may give rise to rapid spring brooks or to associated seepage areas (cf. Danks and Williams 1991).

Like the terrestrial habitats, these many kinds of aquatic habitats interdigitate in the Yukon landscape in a complex mosaic that provides diverse opportunities for insects. Aquatic habitats in this northern and mountainous region are characteristically cool, and well supplied with water especially during snowmelt. Moreover, habitats prevented from draining away by permafrost and supplied with meltwater have relatively stable temperatures and water supply, together with relatively slow evaporation. They are more stable than comparable small pools farther south.

The widespread small rich lentic habitats, especially sun-warmed pools, support many Yukon species of dytiscids, dragonflies, caddisflies and chironomids. Shallow transient snowmelt pools support limnephilids (Wiggins and Parker 1997) as well as mosquitoes. Bogs, including bog pools, fens and marshes have distinctive species of dragonflies (Cannings and Cannings 1997), chironomids (Oliver and Dillon 1997), dytiscids (Larson 1997),

sphaerocerids such as *Pullimosima dahlia* (Duda) (Marshall 1997), caddisflies such as *Limnephilus diphyes* McLachlan and *Sphagnophylax meiops* Wiggins and Winchester (Wiggins and Parker 1997), and anthomyiids (presumably including *Delia diluta* (Stein): Griffiths 1997). The dragonfly *Somatochlora sahlbergi* Tryböm lives in deep, cold ponds with aquatic moss (Cannings and Cannings 1997). Cold lakes have relatively few species, though they have not been well investigated, but nevertheless support some distinctive species such as the caddisfly *Molanna flavicornis* Banks (Wiggins and Parker 1997). The fauna of cool streams is quite rich in stoneflies and certain caddisflies. Some characteristic stoneflies are hyporheic, living deep in the gravel of the stream bed and appearing at the substrate surface only just before emergence, as in species of *Isocapnia*, *Alaskaperla*, *Paraperla* and *Suwallia* (Stewart and Ricker 1997). Several Yukon insects are associated or probably associated with springs, including dytiscid beetles such as *Agabus austini* Sharp (Larson 1997) and *Perlomyia* stoneflies (Stewart and Ricker 1997).

Habitat choice is restricted by additional microhabitat requirements. For example, the dragonfly *Leucorhinia patricia* Walker requires floating moss mats (Cannings and Cannings 1997); most *Dicosmoecus* caddisflies are restricted to clear running water (Wiggins and Parker 1997). Several species show interesting habitat differences in the Yukon compared with the same species farther south. For example, some species of springs and cool streams in the south (which are less stable and would freeze farther north) inhabit rivers and lakes in the north (e.g. caddisflies of the genera *Apatania*, *Ecclisomyia* and *Micrasema*: Wiggins and Parker 1997). Northern-adapted species of chironomids (e.g. *Sergentia coracina* (Zetterstedt), *Tanytarsus gracilentus* (Holmgren)), which occur in arctic ponds, are found in the cold bottom water of deep lakes south of treeline (Oliver and Dillon 1997).

In summary, a very diverse mosaic of habitats is available to species in the Yukon, making the region potentially suitable for a larger number of species than might otherwise be so.

Trophic Relationships and Biological Interactions. The relationships of Yukon insects with food resources and other organisms is of particular interest from 2 viewpoints. First, the fauna might be incomplete (underexploiting certain resources) or certain resources might be limited (restricting certain taxa). Second, the Yukon is a testing ground, as it were, for natural experiments on colonization and competition that would be expected after deglaciation as species entered the Yukon from elsewhere, or as Yukon species moved out of the Beringian refugium (cf. Wiggins and Parker 1997). Consequently, species interactions in the area are of particular interest. Unfortunately, detailed information is very scanty.

The wide range of habitats and microhabitats in the Yukon makes available many potential foods for insects. Species with many different trophic habits live in the region (Table 5 illustrates a small sample), and insects participate in many ecosystem processes, just as they do in more temperate climates. For example, larval caddisflies, stoneflies and chironomids are very important to aquatic food webs in nutrient and energy cycling; some of them comminute organic material. Their adults participate in terrestrial food webs. In soil systems, mites and several kinds of insects serve to comminute and cycle organic material. Nevertheless, some resources in the Yukon are not as plentiful as farther south. Although more than 1112 species of vascular plants occur in the Yukon (Cody 1996), the number of plant species available for herbivores is reduced relative to temperate areas, potentially hindering species that specialize on one hostplant species or genus, such as many curculionids and delphacids (Anderson 1997b; Wilson 1997). In many northern aquatic habitats, the coarse particulate organic matter relied on by shredders and typically contributed by the

TABLE 5. A few examples of the range of food resources exploited by Yukon arthropods.

Trophic habit	Food resource	Examples
Herbivores	Trees	Some Lepidoptera; some Curculionidae
	Monocotyledons	Delphacidae; many Cicadellidae; several Anthomyiidae
	Herbs - leaves, stems	Many Heteroptera; many Lepidoptera; some Anthomyiidae
	-flowers	Some Lepidoptera
	-roots	Some Curculionidae; some Anthomyiidae; some Lepidoptera
Predators	Various other arthropods	Araneae; Odonata; Saldidae; Asilidae; etc.; also some Aculeata, etc.
Saprophages	Dung	Scarabaeidae; some mammal-associated Leiodidae, Staphylinidae and Sphaeroceridae
	Detritus and associated microflora	Several groups of Ephemeroptera, Trichoptera; many Oribatida; Simuliidae
Fungivores	Mushrooms	Some Anthomyiidae; some Sphaeroceridae

leaves of deciduous trees is in short supply, which may limit large shredder stoneflies (Stewart and Ricker 1997). Fine particles of organic matter derived by breakdown of the coarse material (and associated microfungi limited by cold) are likewise reduced in running waters, and so is detritus (Cowan and Oswood 1984). Such reductions may explain a general reduction of filter-feeding caddisflies (Wiggins and Parker 1997). Primary production exceeds decomposition capacity in any event, as evidenced by peat accumulation in many habitats. Filter-feeding species might also be particularly vulnerable in habitats where they would be exposed to icing, unless able to develop rapidly during ice-free periods. Cold headwaters are especially deficient in the fine suspended particles fed upon by typical black flies. Species of the genus *Gymnopsis*, which feed atypically by scraping rather than by filtering, are well represented among Yukon black flies (Currie 1997).

The hostplants used by herbivores vary with the group. In weevils, a substantial proportion of the Yukon species for which hostplants are known eat species of Salicaceae or Pinaceae, the dominant groups of northern woody plants (Anderson 1997b). As expected, similar trends are evident in Yukon species of the primarily tree-associated families Buprestidae, Scolytidae and Cerambycidae (Anderson 1997a). In aphids, most species likewise feed on common trees and shrubs in the Salicaceae, Betulaceae and Pinaceae (Footitt and Maw 1997). In Heteroptera, most herbivores are associated with herbaceous plants, grasses and sedges or northern conifers and shrubs characteristic of the Yukon (Scudder 1997b). Species of the beetle family Byrrhidae, which are relatively well represented in the Yukon (Anderson 1997a), feed on mosses, plants characteristic of northern terrain. Such hostplant associations help to suggest the origins of the Yukon fauna.

Most insect predators take any prey in a suitable size range that they can catch. Consequently, the commonest prey items belong to abundant northern taxa (e.g. adults of the anthomyiid *Alliopsis glacialis* (Zetterstedt) prey on adult chironomids: Griffiths 1997). Presumably, groups or species more specialized to prey on such taxa would be at an advantage. Anderson (1997a) has noted that chironomids and mosquitoes in shallow pools

would provide abundant prey for dytiscid beetles. Indeed, both dytiscid larvae and many such potential prey show characteristic springtime development.

Data from the Yukon about species interactions are relatively limited but suggest some interesting trends. As might be expected, there are indications of competitive differences between related species, at least based on the fact that closely related species seldom occur together. For example, larvae of the stoneflies *Pteronarcys dorsata* (Say) (especially at lower elevations) and *P. californica* Newport (especially at higher elevations) do not occur in the same section of a stream (Stewart and Ricker 1997). There are phenological differences between the large, closely related dragonflies *Aeshna septentrionalis* Burmeister and *A. sitchensis* Hagen (Cannings and Cannings 1997). The fact that related species may have been recorded from the same type of habitat in the Yukon, such as shallow pools, however, does not necessarily mean that they coexist, because general rather than more specific features were used to classify the type of habitats from which species are collected (Larson 1997).

Some organisms characteristic of temperate zones, such as earthworms and hydro-psyhid caddisflies, disappear or are greatly reduced (Behan-Pelletier 1997; Wiggins and Parker 1997). Loss of more southern taxa may reduce certain natural enemies for the taxa that persist northward (e.g. Finnamore 1997 for some parasitoids). Aculeate cleptoparasites are relatively well represented in the Yukon, although this pattern does not necessarily stem from particular biological interactions or advantages but might simply reflect the fact that the cleptoparasitic groups occur predominantly in western North America (Finnamore 1997).

Such changes would be expected to alter species interactions. In any event, because of changes in the number and composition of species, community structure in northern life zones appears to be characteristically different from farther south (Downes 1962, 1964; Danks 1981). In ecosystems of northern Canada, the organization of species into tightly integrated communities is less evident. Danks (1993) pointed out that unbalanced or incompletely exploited systems, where litter accumulates because it is too cold for complete decomposition, where many plants are not seriously attacked by insect herbivores because herbivores are rare, where many sites have not yet been colonized following disturbance (of various scales and frequencies) and where large segments of the year and even of the day are unsuitable for activity, may be qualitatively different from typical southern ones. These general features of northern ecosystems also prevail in the Yukon, indicating that the limitation of certain trophic and biological relationships will help to explain the nature of the fauna. For example, in the Yukon, as already noted, cold wet soils contain relatively few species, relatively little particulate material is available for filter-feeding insects, and species that feed on common plants predominate, apparently at the expense of some more specialized species.

Adaptations. Information about the adaptations of insects to past or present conditions in the Yukon consists chiefly of scattered notes. More extensive information is available on wing reduction or loss (treated above but briefly noted here), and on some elements of seasonal adaptation.

Conditions in northern habitats require adaptations to the limited resources, to the marked seasonality, and to the very severe winters. General adaptations to the limitation and unpredictability of resources of temperature, time and energy include melanism, basking and opportunistic activity and microhabitat choice (which take advantage of locally or temporarily higher temperatures), small size of members of some taxa (which conserves resources,

for example because smaller species of insects typically complete development with a lower heat budget), reduction of mating or mating behaviour (which reduces the need for activity), change and especially reduction of feeding habit (which compensates for the reduced availability of food resources), and parthenogenesis (which may buffer genetic systems against change). These adaptations were discussed by Downes (1962, 1964, 1965) and Danks (1981). Many of them have been reported in Yukon species.

For example, the caddisfly *Oligotricha lapponica* (Hagen) is melanic (Wiggins and Parker 1997). Individuals from Yukon populations of the dragonfly *Sympetrum internum* are very small in size. Diurnal activity is advantageous in arctic and subarctic species (where daylight is continuous or nights are cold); the day-active butterflies are well represented among the Lepidoptera in the Yukon, for example (Table 1) as well as in the arctic more generally. Adults of Dytiscidae, which like most other water beetles characteristically fly at night, would be expected to show adaptations for diurnal activity in the very long days of the Yukon summer. Many insects take advantage of locally warm habitats, and this would be especially important in the Yukon. Indeed, some species are active only when the sun shines (e.g. males of the dragonfly *Somatochlora franklini* (Selys); Cannings and Cannings 1997), and may rely on sun-warmed habitats for adult activity (e.g. asilids, butterflies) or larval development (some dytiscids). Species in which adults fly actively to find food, as in dragonflies, might be at a particular disadvantage in cold regions.

Biting flies dependent on host blood for egg development would likely be at a disadvantage in host-limited northern environments. The Yukon black flies include a high proportion of autogenous species—25%, compared to less than 3% in black flies as a whole—in a range of genera; furthermore, among those supposed to have survived the glacial maximum in Beringia more than 50% of the species are autogenous (Currie 1997).

Parthenogenesis is known or suspected in about 20% of the oribatid mite fauna of the Yukon, and high levels of thelytoky may be correlated with disturbed habitats (Behan-Pelletier 1997). However, the Yukon percentage is close to the percentage for Canadian and North American faunas as a whole (Behan-Pelletier 1997), and parthenogenesis is common in early derived oribatid families. It appears to be a pre-existing rather than an adaptive condition in these mites. Parthenogenesis also occurs in some Yukon weevils (including 2 Beringian species), but again these species, such as the introduced strawberry root weevil *Otiorrhynchus ovatus* (Linn.), belong to groups that include parthenogenetic species elsewhere (R.S. Anderson, pers. comm.). A similar conclusion was drawn that wing reduction in many of the Yukon species that show this feature is typical of their groups (Anderson 1997b). Wing reduction or loss appears to be associated with stable habitats in carabids, delphacids and cicadellids, but there is some evidence of a correlation between wing loss and isolation in Beringian species, especially in Lepidoptera (see Wing Loss and Other Structural Modifications).

A second set of adaptations, to the marked seasonality of northern habitats, includes long life cycles, reduced voltinism and early synchronized emergence (Downes 1962, 1964, 1965; Danks 1981, 1996; Danks et al. 1994). Long life cycles are known in some Yukon species. The life cycle of the dragonfly *Somatochlora sahlbergi* may take 5 years (Cannings and Cannings 1985, 1997). Many species have 2- or 3-year life cycles, including many stoneflies (Stewart et al. 1990; Stewart and Ricker 1997) and some grasshoppers (Vickery 1997). Long life cycles would be expected in other Yukon species, for example some asilids, caddisflies and weevils, based on information from other northern regions. Other groups are characteristically univoltine (e.g. some caddisflies, dragonflies and leafhoppers). In several groups the life cycle is flexible, so that it is univoltine in the north but bivoltine farther south

(e.g. Wilson 1997 for the delphacid *Javacella pellucida* (Fabricius)), or univoltine to the south but takes 1 or 2 years in the Yukon (Stewart and Ricker 1997 for the stonefly *Isoperla petersoni* Needham and Christenson).

A particularly interesting adaptation is the biennial appearance of some butterflies of the genera *Boloria*, *Erebia* and *Oeneis*, and moths of the genus *Xestia*, in which the life cycle lasts 2 years (review by Lafontaine and Wood 1997). In *Xestia*, the 2-year life cycle is controlled by obligatory diapause in the prepupal, and possibly also larval, stages (Lafontaine et al. 1987). Especially interesting too is the fact that in many species emergence of essentially all individuals is synchronized, taking place only in alternate years. Moreover, many species in a region are synchronized with one another, in the Yukon emerging only in odd-numbered years in *Xestia*, and chiefly in odd-numbered years in the butterflies. Alternate-year emergence occurs in similar Lepidoptera from other northern and alpine habitats, and in the northern aradid bug *Aradus cinnamomeus* Panzer (Heliövaara and Vaisänen 1984, 1986, 1988). Mikkola (1976), Wipking and Mengelkoch (1994) and others have supposed that the situation in Lepidoptera resulted from an episode of very severe weather in the past that essentially eliminated the intervening year-class (cf. Hanski 1988). This disruption was coupled with the density-dependent effect of natural enemies, especially parasitoids, that build up in years of abundance and suppress any populations the following year. (The parasitoids would persist that year on co-occurring univoltine species.) The role of hostplant defences has also been hypothesized by Mikkola and Kononenko (1989). The Yukon, with its particular environmental and biological history, would be an ideal place to investigate these phenomena further.

In many northern species adults emerge early in the year and synchronously, using the short growing season to maximum advantage (Downes 1962; Danks and Oliver 1972; Corbet and Danks 1973). Some but not all Yukon species of dragonflies do this, for example (e.g. *Coenagrion interrogatum* (Hagen), *Cordulia shurtleffi* Scudder: Cannings and Cannings 1997). Such life cycles, like the 2-year life cycles, typically are controlled by diapause programmed by environmental cues such as photoperiod (Danks 1987). Such a diapause typically suppresses development until the following spring, preventing emergence during summer (which would be some time after the start of the growing season). Diapause might be expected to be more marked farther north, but in some instances the shorter season and cooler conditions even eliminate the need for it. For example, limnephilid caddisflies from temporary pools in the south pass the summer in adult reproductive diapause while pools are dry; in the north, where the growing season is short, interpolating such an adult diapause might prolong development too much and require a second year of larval growth (Wiggins and Parker 1997). Similar adjustments of development to season length—for example programmed slower larval growth to avoid a second generation likely to fail—are known in various insects from elsewhere (Danks 1994b; Nylin 1994).

A final set of adaptations to northern habitats relates to overwintering and cold hardiness (e.g. Downes 1962, 1964, 1965; Danks 1981, 1996; Danks et al. 1994). The overwintering stage is fixed in most taxa, though there are exceptions, such as the northern dytiscid beetle *Agabus ajax* Fall, which overwinters as an egg (Larson 1994) not as an adult like most dytiscids. Many dytiscids and chironomids survive in frozen habitats. Several other aquatic species, e.g. of Plecoptera and Corixidae, overwinter in unfrozen winter sites; some of them move from less well protected sites to particular unfrozen habitats for overwintering (e.g. Danks 1991). The hyporheic habitats characteristic of many Plecoptera presumably do not freeze. In general, lentic species of aquatic insects are more likely to be freezing tolerant,

whereas apparently many lotic species require unfrozen winter habitats (review by Oswood et al. 1991).

Physiological resistance to cold itself appears to be most marked as a taxonomic character in groups such as Chironomidae that evolved in cool habitats (e.g. Danks 1971). However, individual species that are especially cold hardy in a given group might be expected to have survived in Beringia, rather than in southern refugia like their less cold-hardy relatives (cf. Wiggins and Parker 1997). In contrast, dragonflies cannot survive in frozen habitats, and their distribution accords approximately with the boundary of continuous permafrost.

Finally, successful survival in seasonally cold habitats requires many simultaneous adaptations, not only for cold hardiness, but also for seasonal timing and control, water balance, metabolism and energy budgets (Danks 1996). Stewart and Ricker (1997) point out that many features of Yukon stoneflies are consistent with requirements for adaptations to cold, including small gills, nymphal development in unfrozen habitats, extended voltinism and diapause, seasonal timing of feeding, exploitation of certain habitats such as tundra ponds, and capacity for winter emergence, mating and oviposition. Again, Beringian noctuid moths include a number of species with remarkable modifications of eyes, wings, life span and reproductive behaviour, adaptive for life in the arctic (Downes 1964, 1997; Lafontaine and Wood 1988, 1997). Such a suite of requirements reduces the numbers of species that can survive under northern conditions, and gives clues as to why certain groups are more prevalent in the Yukon.

Ecological Correlations. Many adaptations of particular Yukon species, especially to northern environments, were referred to by chapter authors and outlined above. Several ecological features are compared here between insect families that are the best and least well represented in the Yukon (from Table 2). Such a comparison seeks correlations between features of the different groups and their relative success or lack of success in the Yukon. Several features show no correlation, including large, medium or small body size, good or poor dispersal ability, favoured vegetation type (forested or open), and specific adaptations to northern or other conditions. However, the data are not complete and, at least at the family level, all features are shared (though to different extents) by both best and least well represented groups. On the other hand, correlations are visible between Yukon occurrence and “northernness” and some elements of habitat and trophic relationships, as summarized in Table 6. Such ecological information about the Yukon fauna is incomplete; thus, data on parasitoid groups are very limited, but the extremely diverse family Ichneumonidae is very well represented in the arctic (summary in Danks 1981) and many species of parasitoids as well as predators must occur in the Yukon.

Nevertheless, Table 6, although it is based on only 34 taxa and is biased against less well represented groups because of the choice for analysis of taxa with the most Yukon species, shows several interesting trends. First, northern or widespread groups dominate the well represented set of taxa: 17 of 19 (89%) of such taxa (listed in the top half of the table) are northern or widespread, versus only 6 of 15 (40%) of less well represented taxa. In other words, success in the Yukon is related to taxonomic placement. Consequently, features shared by species in the same family, which have a common evolutionary history, must explain much of the taxonomic composition of the Yukon fauna. Many of the best represented groups develop in aquatic or semi-aquatic rather than terrestrial habitats: 13 of the 19 such groups (68%) are aquatic or semi-aquatic versus only 4 of 15 (27%) of the less well represented ones. Nevertheless, some terrestrial groups (e.g. anthomyiids, butterflies) are

TABLE 6. Families of insects best and least well represented in the Yukon, and certain ecological characteristics. For further explanation see text. Abbreviations: North American occurrence. Northern or southern affinity, based on percent of North American spp. in Canada as given in Table 1. Northern or widespread: N, >50%; (N), 34–50%; Southern or restricted: S, <25%; (S), 26–33%. Habitat of larva. A, Aquatic; S, Semiaquatic; T, Terrestrial. Habitat type. L, lentic (standing, including very slow moving, waters); R, lotic (running waters); LR, both more or less equally; Lr, both, mainly lentic. Trophic type. D, Detritivore; H, Herbivore; mH, Microherbivore (e.g. algae); P, Predator (includes parasitoids, etc.); Sa, Saprovore; Sh, Shredder.

Taxon	Percent of Canadian spp. in Yukon (from Table 1)	North American occurrence	Habitat of larva	For aquatic spp., predominant habitat type	Predominant trophic type
Nymphalidae	52	N	T	–	H
Phryganeidae	50	N	A	L	Sh-D-H-P
Saldidae	46	N	S	(LR)	P
Anthomyiidae	44	N	T	–	Sa-H-P
Dytiscidae	43	N	A	Lr	P
Pieridae	43	N	T	–	H
Chloroperlidae	41	N	A	R	P
Limnephilidae	41	N	A	LR	D
Anthocoridae	40	(N)	T	–	P
Aeshnidae	38	N	A	L	P
Capniidae	37	(N)	A	R	Sh-D
Nemouridae	37	N	A	R	Sh-D
Corduliidae	34	N	A	LR	P
Simuliidae	34	N	A	R	mH
Arctiidae	27	(S)	T	–	H
Leptoceridae	27	N	A	Lr	D-H-P
Sphecidae	25	S	T	–	P
Rhyacophilidae	24	(N)	A	R	P
Leuctridae	24	(N)	A	R	Sh-D
Asilidae	16	S	T	–	P
Lygaeidae	16	(N)	T	–	H
Vespoidea	16	S	T	–	P
Corixidae	15	N	A	Lr	P
Glossosomatidae	12	(S)	A	R	mH
Acrididae	11	S	T	–	H
Noctuidae	11	N	T	–	H
Tingidae	11	S	T	–	H
Coenagrionidae	10	(N)	A	LR	P
Curculionidae	10	S	T	–	H
Hesperiidae	9	S	T	–	H
Pentatomidae	9	(S)	T	–	H
Sphingidae	9	(N)	T	–	H
Hydroptilidae	7	(S)	A	LR	mH
Notodontidae	6	(N)	T	–	H

well represented too. Such an increase in aquatic species at the expense of terrestrial ones is well known in the arctic (e.g. Danks 1990, fig. 4), and appears to reflect the greater warmth and stability of aquatic habitats in severe environments.

For aquatic species, the occurrence of lentic and lotic forms is about the same in both well and less well represented taxa (Table 6). However, there are clear differences from group to group. In particular, lentic species dominate the well represented dytiscid fauna of the Yukon (Larson 1997), which contains more than 40% of the Canadian species of Dytiscidae (Table 6); most of the Yukon species are widely distributed northern boreal forms. Likewise, in mosquitoes, with many species widely distributed in lentic habitats, about 30 species have been reported from the Yukon (Belton and Belton 1990), 40% of the

74 Canadian species (Wood et al. 1979). Again, lentic Trichoptera are relatively well represented in the Yukon (Wiggins and Parker 1997). Lotic Trichoptera are less well represented, perhaps because of a lack of certain food resources (Wiggins and Parker 1997). In contrast, most species of stoneflies and black flies are lotic, and—as expected—so are the Yukon species. In these groups, the Yukon fauna appears to have been derived chiefly by invasions from the south of species from the lotic montane habitats of the Cordillera.

Data on the predominant trophic types, shown in Table 6, again suggest differences between the well and less well represented taxa. Thus, 8 of 19 (42%) of the well represented taxa contain chiefly predatory species, compared to only 4 of 15 (27%) of less well represented taxa. Predatory species likewise are conspicuous in the Yukon beetle fauna as a whole (Anderson 1997a). Spiders (all predatory), especially the ground-dwelling families, also are relatively well represented in the Yukon (Table 3). On the other hand, only 3 of 19 (16%) of well represented taxa (50% of terrestrial groups) contain chiefly herbivorous species, compared to 9 of 15 (60%) (82% of terrestrial groups) for the less well represented ones. A general reduction of herbivores is also clear in arctic compared to temperate species (e.g. Downes 1962; Danks 1981, 1986).

The ecological correlations revealed by this general analysis, and the more detailed evidence discussed in previous subsections, reveal some of the ways in which the composition of the Yukon fauna is related to the habitats characteristic of the area.

Distributional Patterns

Most authors have grouped the distributions of species from the Yukon into range types that accord with the geographical areas customarily used in zoogeographic analysis. Moreover, certain restricted distributions occur repeatedly in species from the Yukon, and authors have independently grouped species into characteristic northwestern North American or other range types. The prevalent range types differ among groups, and hence authors in different chapters have highlighted different types, including zonal as well as geographical groupings. Therefore, it is not always possible to compare the information directly. Nevertheless, an attempt is made here to compare the occurrence of certain range types by extracting data directly from the annotated lists when not already summarized in this way by authors. Many range types reflect the importance of the ice-free area of Beringia and its isolation during the late Pleistocene by glaciers from the rest of North America.

Characteristic range types are exemplified in Figs. 3–11. Each figure shows the range of a sample species included in a particular range type, but the figures have not been generalized to show the whole of the geographical areas (summarized below) that might be occupied by one or another species with a given type of range.

On a broad scale, species with *Holarctic* ranges occur broadly in both the Nearctic and Palearctic regions (Fig. 3). Species with *Nearctic* ranges, discussed separately below, are found in North America only. Species with *Other* broad range types are found also in other biogeographic regions.

On a smaller scale, many species that occur in the Yukon are confined essentially to regions unglaciated in Pleistocene time, and hence are of particular interest in the context of the Beringian refugium. *Beringian* species occur, whether narrowly or widely, somewhere in Beringia, usually taken as west of the Mackenzie River and north of the Tintina Trench (though more widely for some more mobile groups) in North America, and east of the Lena River (or by a narrower definition the Kolyma River) in Eurasia. Some authors favour this general term even for species recorded from only a small part of Beringia, because they believe that the species are more widely distributed than current records show (cf. Griffiths

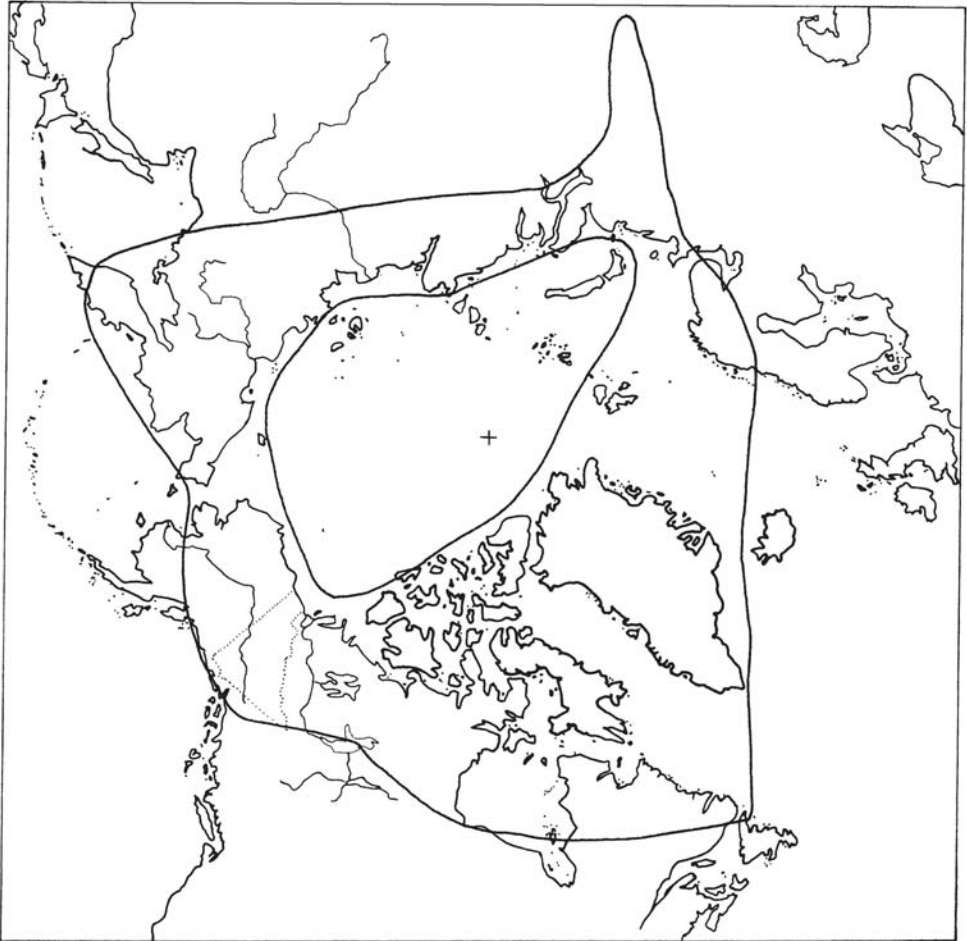
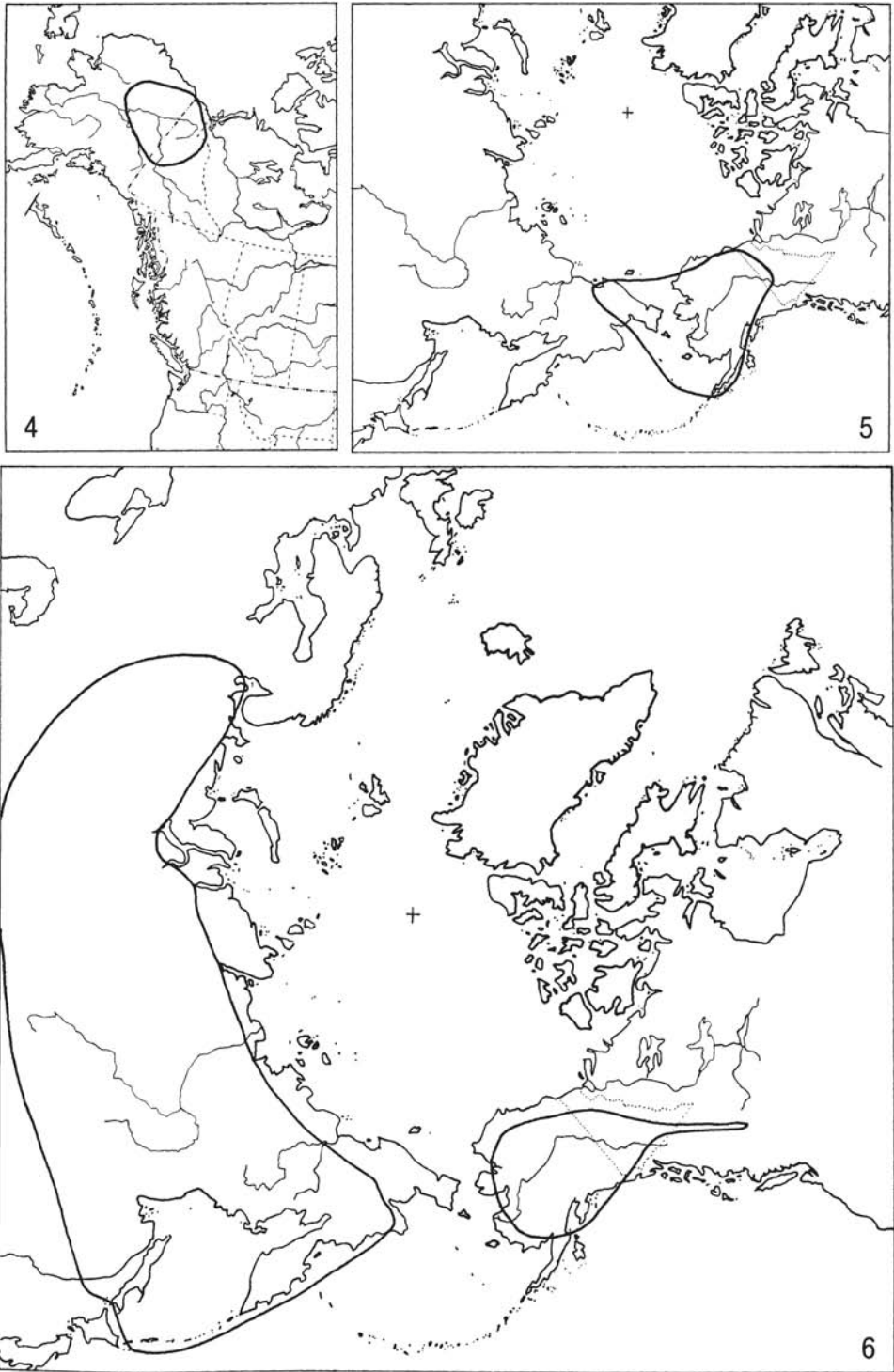


FIG. 3. Range types of Yukon species: Holarctic, exemplified by the circumpolar arctic mosquito *Aedes nigripes* (Zetterstedt) (after Danks 1981).

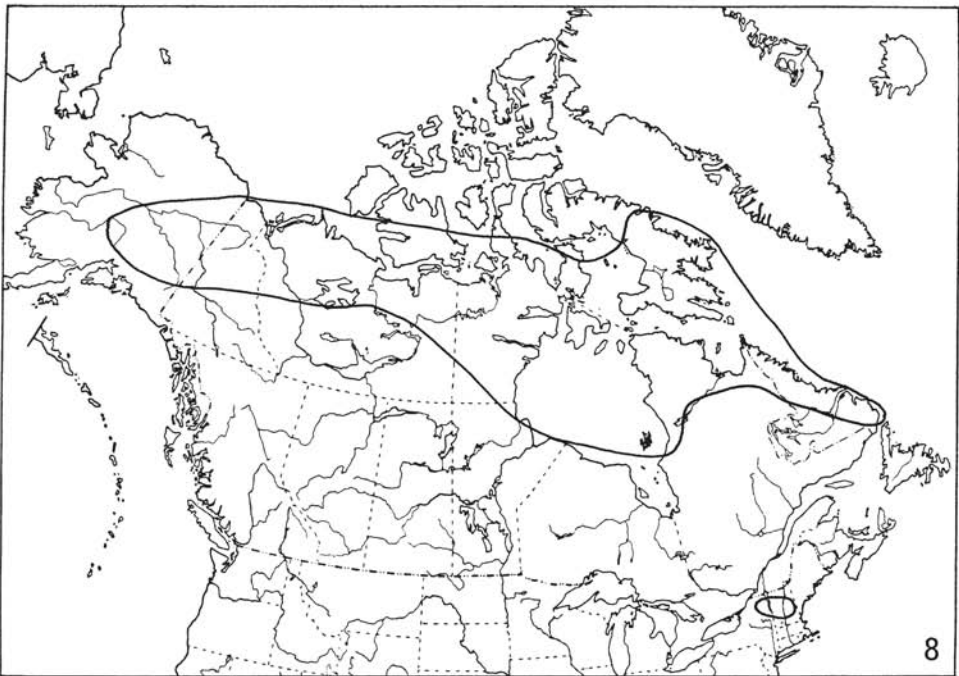
1997). However, other authors distinguish range types within Beringia. *East Beringian* species (Fig. 4) occur in unglaciated northwestern parts of North America only. *East-West Beringian* species (Fig. 5) occur there and also in the unglaciated northeastern parts of Eurasia. *Palaeartic-East Beringian* species (Fig. 6) are widely or very widely distributed in the Palaeartic but narrowly restricted in the Nearctic region to East Beringia. More or less widespread Nearctic species otherwise found only in West Beringia (*Nearctic-West Beringian*), such as the leafhopper *Psammotettix lividellus* (Zetterstedt) (Hamilton 1997), are much less common in most groups.

The fact that some Nearctic, and even Holarctic, species, even though widely distributed in North America, do not occur in the unglaciated parts of the Yukon is also of interest (see Ranges Excluding Beringia).

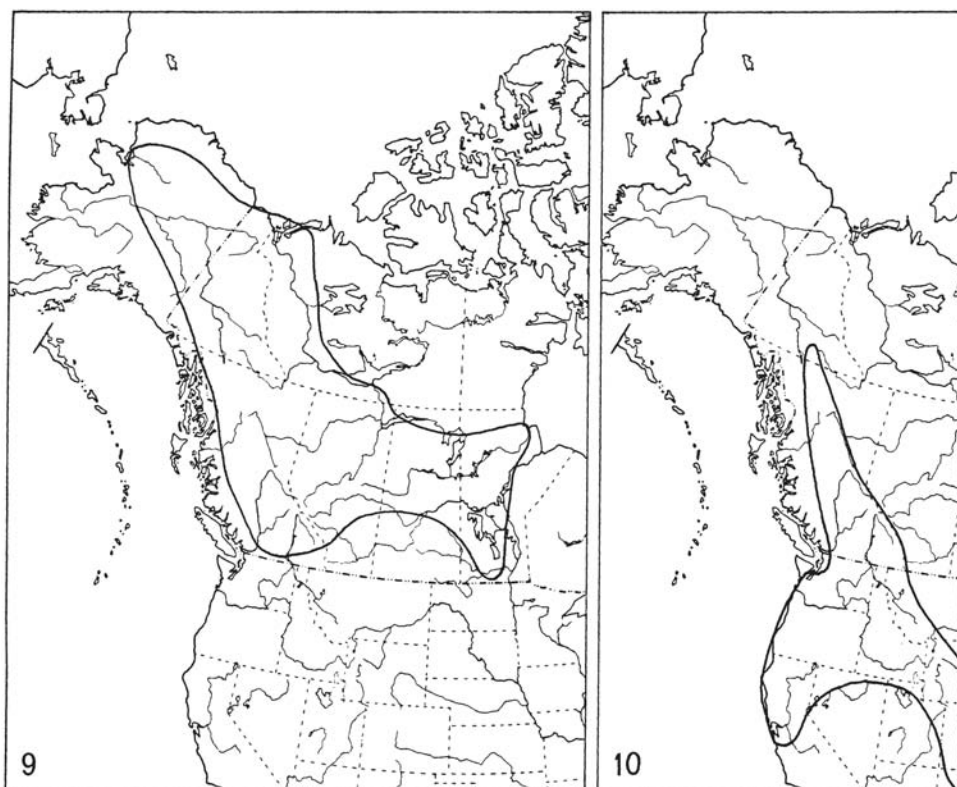
For Nearctic species from the Yukon, occurrences to the east and to the south, across and beyond the regions of Pleistocene ice fields, are especially interesting. Many typical *Widespread Nearctic* species occur across the continent (Fig. 7). Many *Northern Nearctic* species are transcontinental or nearly transcontinental, but occur only in northern North



FIGS. 4–6. Range types of Yukon species: 4, East Beringian, exemplified by the mirid bug *Labops chelifer* Slater (after Scudder 1997); 5, East-West Beringian, exemplified by the noctuid moth *Xestia alaskae* (Grote) (after Lafontaine et al. 1983, with Yukon records added); 6, Palearctic-East Beringian, exemplified by the asilid fly *Lastopogon hinei* Cole and Wilcox (after Cannings 1997).



FIGS. 7–8. Range types of Yukon species: 7, Widespread Nearctic, exemplified by the asilid fly *Cyrtopogon bimaculata* (Walker) (after Cannings 1997); 8, Northern Nearctic, exemplified by the arctic carabid beetle *Pterostichus arcticola* Chaudoir (after Ball and Currie 1997)—note that there is also a disjunct population in the northern Appalachians.



FIGS. 9–10. Range types of Yukon species: 9, Western Nearctic, exemplified by the dytiscid beetle *Agabus audeni* Wallis (after Larson 1997); 10, Cordilleran, exemplified by the asilid fly *Laphria vivax* Williston (after Cannings 1997)—note that the range of this particular species excludes Beringia.

America (Fig. 8); such northern species are evident in Dytiscidae, for example (Larson 1997). *Western Nearctic* species (Fig. 9) are confined to areas west of the 100th meridian or of Hudson Bay, while *Cordilleran* species (Fig. 10) are confined to the Cordillera, west of the Mackenzie River. Many *Nearctic excluding Beringia* species are widely distributed but nonetheless are absent from the area of East Beringia (Fig. 11). Such species, typically more southern, have been noted especially by Griffiths (1997) and Scudder (1997b). Finally, several species have *Disjunct* ranges of various kinds (cf. Fig. 8), with subpopulations that apparently or actually are geographically separated. The significance of the different range types is discussed further in the final section of this chapter.

Ranges can be identified alternatively in association with zones, biomes, or major habitats, such as arctic/tundra or boreal/boreal forest. Such a characterization emphasizes the north-south differences in environments, rather than the geographical associations as such, though comparison between the two provides useful information.

Synopsis of Ranges. The relative representation of Beringian and other range types is shown in Table 7 for species recorded from the Yukon Territory in this book. As explained earlier, data for some groups are less reliable than for others, and even in some taxa where most aspects of ranges are adequately known (e.g. Anthomyiidae) it is not possible to



FIG. 11. Range types of Yukon species: Nearctic excluding Beringia, exemplified by the dytiscid beetle *Agabus seriatus* (Say) (after Larson 1997).

distinguish East Beringian from East-West Beringian species reliably because data from eastern Eurasia are so incomplete.

Table 8 is a summary of the data for taxa listed in Table 7, showing the percentage representation of Nearctic-plus-Palaeartic, Beringian, and Nearctic species for spiders, oribatid mites and insects as a whole. In spiders, many species occur in both the Nearctic and Palaeartic regions, including a significant number of Nearctic-West Beringian (including Cordilleran-West Beringian) species. Although knowledge of mites is especially inadequate, many Holarctic species are recorded among the oribatids from the Yukon. In insects as a whole (Table 8) and in most individual insect taxa (Table 7) there are more than twice as many Nearctic as Nearctic-plus-Palaeartic species. However, the latter clearly outnumber Nearctic species in Anthomyiidae, and apparently in Chironomidae from the North Slope, although species from these northern collections would be expected to have more Holarctic species (see Zonal/habitat Ranges).

Spiders restricted to Beringia comprise about 5% of Yukon spiders (Table 8). Overall, insect species restricted to Beringia (cf. Figs. 4, 5) comprise about 7% of the total number of species (Table 8), but are especially well represented in carabids (28/206, 14%: Table 7). Good representation for oribatid mites (29/132 described species, 22%) and delphacids (7/30, 23%) is based on much more limited data. Species restricted to Beringia are much less prevalent in several groups, including the relatively well collected Odonata (0%), Heteroptera (3/208, 1%) and Dytiscidae (2/113, 2%).

TABLE 7. Synopsis of range types in Yukon species. Data from preceding chapters, but in many cases extracted from annotated lists of species rather than from author summaries. Data are especially deficient for groups marked [?]

Taxon	No. of spp. with known ranges	Range type				
		Nearctic plus Palaeartic and others	Palaeartic- East Beringian	East-West Beringian	East Beringian	Other Nearctic
ARACHNIDA						
Araneae	297	147	24	11	3	112?
Acari: Oribatida [?]	132	84	0	8	21	0
INSECTA						
Ephemeroptera [?]	30	4	0	0	0	26
Odonata	33	6	1	0	0	26
Plecoptera	71	3	0	4	1	63
Orthoptera	17	2	0	0	1	14
Heteroptera	208	59	7	1	2	139
Homoptera: Aphidoidea [?]	47	10	1	0	0	36
Cicadellidae	145	23	5	2	13	102
Delphacidae [?]	30	5	10	2	5	8
(All Coleoptera)	910	204	35	23	56	592)
Coleoptera: Carabidae	206	51	5	12	16	122
Curculionidae	59	13	4	2	5	35
Dytiscidae	113	38	3	0	2	70
Diptera: Anthomyiidae	131	74	14		8?	35
Asilidae	20	2	1	0	3	14
Chironomidae [?]	68	55				
Simuliidae	55	16	7	0	3	29
Sphaeroceridae [?]	59	16	8?	0	7?	28
Lepidoptera:				15	18	219
Macrolepidoptera	382	124	6			
Microlepidoptera [?]	136	42	3	1	4	86
Trichoptera	145	28	13	1	5	98
Hymenoptera: aculeate						
wasps, excl. ants	139	20	0	0	1	118
Formicidae [?]	15	1?	0	0	0	14?
Total ¹	2256	561	96	39	111	1449

¹Insect groups except those marked [?]

Nearctic Ranges. Table 9 summarizes range types within the Nearctic region, for the taxa for which data given in previous chapters are sufficiently detailed. Where possible, Wide-spread species (cf. Figs. 7, 8) and Western species (cf. Fig. 9) have been distinguished and within the latter group, if feasible, Cordilleran species (cf. Fig. 10). Overall, more than half of these Nearctic species are widespread, more than a third are Western, and the remainder

TABLE 8. Synopsis of Beringian and other range types in Yukon species (summarized from numbers in the first two lines and the last line of Table 7).

	Number of species with known ranges	Percentage of species		
		Nearctic plus Palaeartic and others	Beringian (endemic)	Nearctic
Araneae	297	58	5	38
Oribatida	132	64	22	14
Insecta (more reliable data only)	2256	29	7	64

TABLE 9. Synopsis of Nearctic range types in Yukon species. Data from preceding chapters, but in many cases extracted from specific ranges given in annotated lists of species rather than from author summaries. Data are especially deficient for groups marked [?]

Taxon	No. of spp. with known Nearctic ranges	Range type				
		East Beringian	Cordilleran	Total Western	Other Western	Wide-spread
ARACHNIDA						
Araneae	115	3	16	25	9	87
Acari: Oribatida [?]	40	21		?		?
INSECTA						
Ephemeroptera [?]	26	0		14		12?
Odonata	26	0	2	5	3	21
Plecoptera	64	1		61		2
Orthoptera	15	1	2	3	1	11
Heteroptera	141	2	23	47	24	92
Homoptera: Aphidoidea [?]	36	0	4	12	8	24
Cicadellidae	115	13	1	34	33	68
Delphacidae [?]	13	5		2		6
(All Coleoptera	648	56	94	205	111	387)
Coleoptera: Carabidae	138	16		?		?
Curculionidae	40	5	2	6	4	29
Dytiscidae	72	2	7	17	10	53
Diptera: Anthomyiidae	39	8	18	20	2	15
Asilidae	17	3	9	9	0	5
Chironomidae [?]	13					
Simuliidae	32	3	17	17	0	12
Sphaeroceridae [?]	35	7	2?	12	10	16
Lepidoptera (part [?])	327	22		114?		191?
Trichoptera	103	5	32	38	6	60
Hymenoptera: aculeate						
wasps, excl. ants	119	1		36		82
Formicidae [?]	14	0		4?		10?
Total¹	1646	115 (7%)		589 (36%)		946 (57%)

¹Insect groups except those marked [?]; percentages remain the same if Lepidoptera (partly [?]) are excluded.

(average 7%) are confined to East Beringia. Some groups, such as Odonata, Aphidoidea, Dytiscidae and Curculionidae, have many widespread species. However, Ephemeroptera and Plecoptera are much more western than average. For a still smaller data set, the proportion of Cordilleran species varies widely among groups; it is especially high in some families of Diptera (Simuliidae, Asilidae and Anthomyiidae) and Trichoptera, as well as apparently in Ephemeroptera and Plecoptera. These general characterizations are helpful for interpreting the historical affinities and habitats of particular groups.

Beringian Ranges and Beringian Extensions. Because range restrictions in the absence of considerable barriers would not be expected, other things being equal, species restricted to East Beringia or East-West Beringia must be regarded as surprisingly numerous (cf. Tables 7, 8). Similar restrictions within North America are evident from the occurrence in many groups of Palaearctic-East Beringian species, which do not extend outside Beringia in the Nearctic region. However, the complementary Nearctic-West Beringian range type is not common in most taxa, although several species of this type do occur in Cicadellidae and in spiders, for example. Part of this uncommonness may stem from lack of data. However, most of it can be explained historically (see Range Types in the concluding section below).

TABLE 10. Occurrence in selected taxa of Nearctic species present in the Yukon but absent or nearly from the unglaciated parts (Nearctic excluding Beringia). Data available directly for some taxa; extracted from ecoregion and other information in annotated lists for others.

Taxon	No. of Yukon spp. with known Nearctic ranges	No. of these Yukon spp. not in Beringia
Ephemeroptera	26	10
Odonata	26	7
Orthoptera	15	3
Heteroptera	141	44
Cicadellidae	115	10?
Carabidae	138	37
Dytiscidae	72	22+
Asilidae	17	8
Anthomyiidae	39	4
Trichoptera	103	20+
Total	691	165+

Ranges Excluding Beringia. A large number of species that occur in the Yukon are present only in the glaciated or non-Beringian portion of the southern Yukon, including species widely distributed in North America (cf. Fig. 11), as well as some Cordilleran species (cf. Fig. 10). Table 10 summarizes data for Nearctic species of selected taxa from the Yukon; for these taxa, about one quarter of the species do not occur in Beringia, and such ranges also are common in some other groups, such as Plecoptera, not shown in the table. In a simple geographical sense, this restriction of species to the southern Yukon is a mirror image of the restrictions of Beringian species to the northern Yukon as just noted. Neither type of species has spread farther despite the absence of conspicuous barriers.

Disjunct Ranges. Several Yukon species have disjunct ranges (cf. Fig. 8). Some of these ranges undoubtedly result merely from collecting deficiencies (e.g. some of the species treated by Finnamore 1997, Lafontaine and Wood 1997 and Marshall 1997; and see Weaknesses of the Data), but others can be expected to reflect real or natural disjunctions, albeit with several different origins of ecological or historical significance. The most common disjunctions in Yukon species (Table 11) are between the Yukon and eastern Canada and between the Yukon (with or without other northwestern areas) and the southern United States. Both kinds include instances of wide disjunctions between Yukon populations and isolated relict populations on eastern or southern mountains. Some other species, though not yet known in the Yukon, are widely disjunct in Alaska from their distributions elsewhere (cf. McCafferty 1985 as cited by Harper and Harper 1997). Wiggins and Parker (1997) suggested that the caddisfly *Limnephilus ornatus* Banks is disjunct in Alaska from its more eastern range.

Zonal/habitat Ranges. Zonal ranges specified by authors for some taxa (again, those with available information) are summarized in Table 12. The table presents only generalized information because the zonal or habitat classifications used by different authors are not exactly equivalent. Nevertheless, this sample shows clearly that, in the Yukon, boreal/boreo-montane species dominate in most taxa (Footitt and Maw 1997; Hamilton 1997; and others), even in Lepidoptera where boreal species have not been well collected (confer Lafontaine and Wood 1997). Significant numbers of widespread species occur in many zones, and, as might be expected in this northern area, arctic species are well represented relative to most other parts of North America at the expense of more southern species.

TABLE 11. Examples of species with real or apparent range disjunctions between populations in the Yukon (or Yukon-Western Canada) and populations elsewhere.

Species	Disjunction between Yukon and:	Reference
Eastern North America		
<i>Arctopsyche grandis</i> , <i>Wormaldia gabriella</i> , <i>Goera tungusensis</i> (Trichoptera)	Northern Quebec	Wiggins and Parker 1997
<i>Delphacodes dentipennis</i> (Delphacidae)	Eastern North America	Wilson 1997
<i>Aptilotus spatulatus</i> , <i>Phthitia quadricercus</i> , <i>Pseudocollinella caelobata</i> , <i>Pteremis wirthi</i> , <i>Rudolfina digitata</i> , <i>Spelobia algida</i> , <i>S. frustrilabris</i> (Sphaeroceridae)	Eastern North America	Marshall 1997
<i>Empoasca spira</i> , <i>Macrosteles slossonae</i> (Cicadellidae)	Eastern North America	Hamilton 1997
<i>Delia groenlandica</i> (Anthomyiidae)	Eastern North America	Griffiths 1997
Southern or West-central North America		
Many species of dune/steppe Lepidoptera, e.g. <i>Schinia persimilis</i> (Noctuidae)	Great Basin/Great Plains	Lafontaine and Wood 1997
<i>Tychius tectus</i> (Curculionidae)	Western and central prairie	Anderson 1997b
Many aculeate wasps (49 spp.)	Southern U.S.	Finnamore 1997
<i>Delia cilifera</i> (Anthomyiidae)	Central Mexican highlands	Griffiths 1997

Particular zonal ranges tend to accord with some of the geographical ranges specified in Table 7, as shown in Table 13. The table shows very clearly that among the species of more northern zones, and especially arctic species, a greater proportion occurs in the Palaearctic plus Nearctic regions, rather than in the Nearctic region alone. This conclusion confirms the similar conclusion drawn by many authors from data for arctic and boreal zones (reviewed by Danks 1981 and Danks and Footitt 1989; see also Mikkola et al. 1991). It is

TABLE 12. Zonal/habitat ranges of Yukon species, in certain groups with available data. Differences among treatments by different authors prevent some groups from being scored, or scored in detail, for this purpose, so that only general trends are represented here.

Taxon	Number of species in zone							Total (known ranges)
	Arctic/subarctic/tundra	Arctic plus boreal/boreo-montane	Boreal/boreo-montane/forest/shrub	Steppe/dune/grassland	Southern/transition/austral	Other zones/habitats	Several/many habitats/wide-spread	
Araneae	132	(incl.)	154					286
Odonata			26		3		4	33
Cicadellidae	9	12	58	(incl. in boreal)	17		49	145
Carabidae	25	6	28	31		98	18	206
Dytiscidae	12	9	72	3			16	112
Curculionidae	2		25	5		11	16	59
Staphylinidae	16		61			97	5	179
Asilidae			11	1		1	7	20
Lepidoptera	135?		338?	45?				518

TABLE 13. Percentages of insect species in given zones/habitats that have particular geographic range types (based on data for Odonata, Cicadellidae, Carabidae, Dytiscidae, Curculionidae, Asilidae: compare Tables 8, 12).

Zone/habitat	Total no. of spp. in each zone	Percentage of species with range type			
		Palearctic plus Nearctic	Palearctic-East Beringian	Beringian (endemic)	Nearctic
Arctic/subarctic and Arctic/boreal	76	45	3	32	21
Boreal/boreomontane and steppe/dune/grassland	282	22	2	5	72
Southern (transition/austral)	20	5	0	15	80
Several/many zones/habitats	96	23	3	5	69

consistent with the greater extent of continuous suitable habitat in northern life zones, especially those with limited vegetation structure, and with the resulting potential for easier dispersal. Conversely, only a small percentage of species from more southern zones (5% in Table 13) occurs also in the Palearctic region. In addition, as might be expected, Beringian species (confined to the northern Yukon) are best represented in the northernmost zones (32%), compared to only 5–15% elsewhere.

Status and Development of the Yukon Fauna

In this section, we attempt to set the fauna of the Yukon into context with the many ecological constraints and effects of regional climatic history that influence and have influenced it. Evidence of many different kinds is available especially from the preceding chapters, albeit typically incomplete, and moreover the most important influences on the fauna differ from taxon to taxon. After a brief overview of these kinds of evidence, we highlight some of the key findings, leading to a synopsis of the main components of the fauna of the region and of its development.

Kinds of Evidence. Explanations for faunal composition and history rely on the kinds of evidence listed in Table 14. Information on past conditions, including potential barriers to insect dispersal and especially the conditions in Pleistocene Beringia, helps to show what could have survived in or passed through lands adjacent to the Yukon Territory. Insect fossils give direct evidence of the presence of such species. The process of faunal development can be estimated especially from systematic and distributional information. For example, relationships among species and populations, and their current ranges, suggest how insects moved and diverged in response to changes over time. Information on dispersal abilities, habitats, and other biological evidence such as ecological valency, together with information on current conditions, helps to interpret these events.

Past Conditions and Glaciation. A first set of evidence, derived largely from geology (see Matthews 1979; Matthews and Telka 1997), establishes a temporal framework for the existence of areas inhabited by insects on 3 time scales. On the longest time scale, the ancient separation and evolution of the continents (cf. Irving 1977) determined whether even high-level taxa were present in North America; some early, especially southern, lineages do not occur anywhere there, including the Yukon (e.g. Stewart and Ricker 1997 for antarctic-perlarian stoneflies).

TABLE 14. Summary of types of evidence available to assess the nature of the Yukon fauna.

Information on past conditions
Distant past
Pleistocene conditions
Habitat development
Fossil evidence
Taxonomic differences
Past ranges or occurrences
Past and present barriers to dispersal
Characteristics of the extant fauna
Taxonomic evidence
Number of species
Whereabouts of close relatives
Extent of diversification
Evolutionary rates
Intraspecific differences (disjunctions, degree of difference, variation, hybrids)
Unusual occurrences
Range types
Ranges
Characteristic range types (especially restricted ranges, endemics, disjuncts)
Ranges in relation to current conditions
Sympatry
Dispersal abilities
Habitat evidence
Other biological evidence
Information on current conditions

During a second long period in the Tertiary, until the Pliocene, Eurasia and North America were connected across the Bering area (cf. Matthews 1979). For millions of years, conditions in what is now northwestern North America, when the continents were distinct basically as they are now (and indeed until about 3 ma B.P.), were more temperate and less continental than today (Matthews and Telka 1997).

Events some 2.5 ma B.P. led to the first extensive lowland tundra environments in the area, important for the development of the arctic elements of the Yukon fauna. However, apparently these environments developed only after the forested land bridge at the Bering Strait had already been broken (Matthews and Telka 1997).

Glaciations and related events beginning in the Pliocene some 2.5 ma B.P. but ending less than 10 000 years ago, and their aftermath, provide the shortest of the historical time scales. Because the influence of a more recent event is more likely to be clearly marked in the fauna than that of an older event, changes during the Pleistocene, especially the late Pleistocene, were especially important.

Throughout the Pleistocene, the influence of ice sheets dominated lands in the northern hemisphere. During this period of about 1.5 million years, extensive glaciations were followed by interstadials, with retreat of the ice and in places climates that were warmer than today's (Matthews 1979). Therefore, organisms were subjected to not one but several series of prolonged and severe changes. Although 4 major glaciations were readily recognized initially from North American data, more detailed examinations, and substantial marine and European information, suggest that there were at least 17 ice advances and retreats (Dort 1972; Van Donk 1976; Fink and Kukla 1977).

In any event, during Pleistocene time, major ice sheets covered much of northern North America (cf. Matthews 1979, fig. 2.7; Scudder 1997a, figs. 11–12). An eastern mass, the Laurentide ice sheet, fed especially by snowfall in the northeast, apparently abutted in the west with the Cordilleran ice sheet (spawned by the Cordilleran mountains) near the foothills

of the Rocky Mountains and in the region of the current Yukon-Northwest Territories boundary (cf. McPhail and Lindsey 1970, fig. 2). Particularly significant was the fact that in northwestern North America and in adjacent parts of Eurasia, depending largely on moisture regimens (determining the supply of snow) and on topography, substantial areas remained ice free. However, these regions were cut off from the rest of the continent by the continental glaciers, although the boundary between the 2 ice sheets was intermittently ice free especially prior to the late Pleistocene (cf. Matthews and Telka 1997): the geological evidence for coalescence of the ice sheets (reviewed by Reeves 1973) is very limited. In North America, East Beringia was free of ice throughout the late Wisconsinan. The Yukon comprised only a small part of this area, and the unglaciated area was much more extensive in Alaska. In Eurasia, a moderately extensive area east of the Kolyma River was ice-covered (partly delimiting the Russian Far East from eastern Siberia), but contiguous unglaciated lands continued up to the more substantial barrier of the Lena River and the Verkhoyansk Mountains. Moreover, the ice-free area extended much farther south in Eurasia than it did in North America. Because water was frozen into the ice sheets at that time, sea level was much lower and North America and Eurasia were broadly connected across what is now the area of Bering Strait. It is important to remember, however, that this situation of a broad connected Beringian area was not a fixed one, because the Pleistocene glaciations lasted for one and half million years involving, as already noted, many ice advances and retreats, with corresponding changes in drainages, the establishment or disappearance of barriers to organisms, and the continuity and suitability of habitats. Despite this complexity, glaciation and its subsequent recession are clearly marked by the fossil and extant fauna. For example, fossil evidence for the Yukon during the last interglacial period (Ch'ijee's Bluff, about 125 ka B.P.) shows that several species were present that are characteristic of more southern sites today, such as the carabid beetles *Bradycellus lecontei* Csiki and *Dyschiriodes* (formerly *Dyschirius*) *laevifasciatus* Horn, and that no species was an obligate tundra inhabitant (Matthews and Telka 1997). Consequently, the relatively short interglacial interval between successive glaciations had relatively warm conditions and suitable habitats for these species.

Evidence from the mid-Wisconsinan (80–30 ka B.P.) likewise suggests a diverse fauna, one more northern than during the interglacial but still apparently representing a climate warmer than today's (Matthews and Telka 1997).

The final recession of the ice sheets, from about 30 000 until less than 10 000 years ago, particularly the Laurentide ice sheet that melted quite rapidly especially from the Great Plains, perhaps provided an early corridor (though a habitat of uncertain suitability for insects) between unglaciated Beringia and more southern parts of North America. Since that time, changes have continued. During the so-called Hypsithermal, a warming interval that was earlier in the northern Yukon (10 ka B.P.) than in the rest of North America, several insects, including some elaterid and cantharid beetles, moved northward beyond their present ranges (Matthews and Telka 1997). The current period is regarded as an interglacial rather than a situation of long-term equilibrium. Matthews (1979), Matthews and Telka (1997) and Schweger (1997) consider it likely that the vegetation and fauna of northern North America have not yet stabilized to the changed conditions.

Beringian Habitats. The nature of Beringia during the last full glacial (24–14 ka B.P.) is especially relevant to the potential survival of insects at that time in the Beringian refugium, and a variety of geological, palaeobotanical and biological evidence about these habitats is now available (Matthews 1979; Schweger 1997). Beringia had a complex Pleistocene history. Forest-dominated and tundra-dominated habitats appear to have oscillated during

the glacial-interglacial changes (Schweger 1997). During the full glacial, Yukon conditions seem to have been cold and relatively dry. Both dry grasslands, supporting ungulates for example (“arctic steppe”), and tundra (“dry tundra” or “fell-field”) appear to have been present. Despite earlier differences of opinion (reviewed by Schweger 1997), a consensus is emerging that a mosaic of steppe and fell-field habitats was present during the full glacial, and that local vegetation depended on local moisture gradients and other features (Schweger 1997). Such a mixture of vegetation types should not be surprising. Even present-day habitats in the arctic comprise about 2% of topographically favoured, relatively mild and rich, wet sedge/moss meadows, forming “oases” in a larger expanse of drier, colder and impoverished terrain (Babb and Bliss 1974).

Insect faunas would have adjusted to these glacial-interglacial habitat changes, although the floral and faunal composition of the actual communities apparently had no modern analogues (e.g. Matthews 1979). Nevertheless, the variety of full-glacial fossil insects (Matthews and Telka 1997)—though dominated by distinctly northern species—and the nature of the current faunas, confirm that habitats were relatively diverse. Such evidence, from both current collections and fossils, depends on the fact that most insects are not particularly adaptable, and tend to be associated consistently with the same habitat type. If the habitat changes, they typically move rather than change (see Composition of the Fauna). The habitat preferences of species currently restricted to Beringia therefore can be assumed to reflect conditions during the late Pleistocene. Some of these species are characteristic of cold, open habitats and tundra, as in Beringian species of weevils (Anderson 1997*b*) and anthomyiids (Griffiths 1997). Many northern Yukon chironomid species come from cold streams as well as other habitats (Oliver and Dillon 1997). Beringian black flies confirm that suitable upland streams existed in Beringia (Currie 1997). There are wet-tundra species of oribatid mites, sphaerocerids, heteropterans and caddisflies (Behan-Pelletier 1997; Marshall 1997; Scudder 1997*b*; Wiggins and Parker 1997). Many Lepidoptera restricted to Beringia, as well as several Beringian species of spiders and leafhoppers and the sphaerocerid *Pullimosima yukonensis* Marshall, inhabit dry tundra (Dondale and Redner 1997; Hamilton 1997; Lafontaine and Wood 1997; Marshall 1997).

A second group of Yukon species is characteristic of grasslands. Such species (especially from dry, warm south-facing slopes) occur in Heteroptera (Scudder 1997*b*) and leafhoppers (Hamilton 1997). The extensive fauna of Yukon grassland leafhoppers led Hamilton to suppose that such grasslands must have been extensive during an interglacial climate significantly warmer than today's. During the Hypsithermal, the main area of continental grasslands likewise extended farther northward than today, and was later replaced by forest (Wright 1976).

The ice-age existence of both grassland and tundra habitats in Beringia is supported by the occurrence of weevils characteristic of both kinds of habitat (Anderson 1997*b*). Specific foodplants of some insect species provide supporting evidence, for example, the dry-tundra *Dryas* and dry-grassland foodplants of certain Yukon Heteroptera, such as the lygaeids *Nysius fuscovittatus* Barber (found on *Dryas*) and *Crophius ramosus* Barber (found on dry *Artemisia* slopes) (Scudder 1997*b*).

Finally, there is even some evidence that pockets of trees or shrubs may have existed; wooded areas are the habitat of the East Beringian weevil *Dorytomus lecontei* O'Brien (Anderson 1997*b*).

In summary, insects characteristic of at least grasslands and tundra survived in Beringia. Consequently, Beringia was not the homogenous barren place of some popular accounts. It was suitable for insect species occupying several different kinds of habitats.

Barriers and Dispersal. The movement of organisms, both on a small scale and in response to massive environmental changes, depends on the existence of habitats that permit survival, that prevent it, and that hinder or prevent dispersal, as well as on the dispersal abilities of the species themselves. For example, the arctic dytiscids of the Yukon that inhabit tundra pools, such as *Hydroporus sibiricus* Sahlberg and *Agabus zetterstedti* Thomson, do not extend into the Cordillera, apparently because suitable lentic habitats are not available there (Larson 1997). Major features that are uninhabitable or difficult to cross, such as mountains and ice sheets, are barriers for most organisms. Several examples in which the ice sheets acted as a barrier to movement of caddisflies were given by Wiggins and Parker (1997), especially for Palaearctic-East Beringian species.

Depending on their nature, extent and continuity, several habitats are barriers for some kinds of organisms but dispersal routes for others (Samways 1994). For example, a major river may intercept weakly flying terrestrial species; only two-thirds of the northern leafhopper fauna has crossed the Mackenzie Valley (Hamilton 1997). However, such rivers could assist dispersal of aquatic forms (Oliver and Dillon 1997), a role further enhanced by connections between drainage systems (e.g. Cobb and Flannagan 1980). Post-Pleistocene movement of black flies along the Cordillera would have been aided by their mountain-stream habitat (Currie 1997). Analyzing the role of such connections is difficult because drainage systems changed everywhere in the period since deglaciation (compare the discussion of McPhail and Lindsey 1970).

In a current Yukon context, the treeline is an important boundary for aculeate wasps (Finnamore 1997), but not for high latitude leafhoppers (Hamilton 1997). Nor is treeline an important boundary for chironomids, but the Arctic Ocean is (Oliver and Dillon 1997). By the same token, forests might have impeded the spread of species adapted to open terrain (e.g. Griffiths 1997 for Palaearctic-Beringian species).

Full-glacial conditions in Pleistocene Beringia appear to have been cold and relatively dry (see the previous subsection), although evidence from the Bering land bridge suggests that moister habitats were widespread (Elias et al. 1996). Only 2 kinds of species would have been able to cross Beringia at that time. First, cold-adapted forms could have lived in or passed through Beringia, such as the caddisfly *Arctopsyche ladogensis* Kolenati (Wiggins and Parker 1997). Second, species with extraordinary powers of dispersal (see below) could have made a rapid crossing.

Species typical of the groups treated in preceding chapters differ widely in dispersal abilities and hence, for example, whether they might currently be able to cross Bering Strait. Most stoneflies (Hynes 1988), caddisflies (Wiggins and Parker 1997), and leafhoppers (Hamilton 1983, 1997) disperse little. Such groups have particular value for biogeographic studies. Nevertheless, even species with limited powers of dispersal can spread if suitable habitats are continuous. Even flightless leafhoppers appear to have spread along the favourable grassland habitats present in Yukon river valleys in the past (Hamilton 1997).

In contrast, dragonflies (Cannings and Cannings 1997) and anthomyiids (Griffiths 1997) easily cross large distances of unsuitable terrain, even oceans, especially where intervening islands can be used as stepping stones. Such groups would have been able to cross the Bering Strait with relative ease.

Finally, of course, the speed of dispersal depends on the distance to be travelled. Presumably, in the absence of barriers (though the Cordilleran ice sheet was relatively persistent) western species moved northward into the Yukon more rapidly than species that would have had to travel much farther from the east (Hamilton 1997).

Taxonomic Evidence. Considerable taxonomic evidence (cf. Table 14), especially that based on careful species-level work, is available to interpret the Yukon fauna.

A first sort of evidence is the numbers of reliably distinguished species in different groups that occur in the Yukon and adjacent areas. The predominance of particular groups suggests that they are favoured by particular conditions in the Yukon. For example, certain northern groups (e.g. Anthomyiidae) and those in certain aquatic habitats (e.g. Dytiscidae, also northern) are especially well represented (see Ecological Correlations, and Table 6). In addition, such groups may have been favoured by the history of Yukon conditions (see below).

A second sort of evidence comes from the relationships between taxa. Relationships at higher taxonomic levels suggest trends in pre-Pleistocene diversification and spread. The closeness of a relationship between North American taxa and their Eurasian relatives suggests whether and how recently they diverged or were separated. Although many species are found on both sides of the Bering Strait (and see Range Types below), this area separates many other closely related species that are different in the Nearctic and Palaearctic regions. For example, 8 sets of North American-Eurasian sister species occur in leafhoppers (Hamilton 1997, table 4). Other examples of such vicariance are the caddisflies *Mystacides longicornis* (Linn.)-*M. interjectus* (Banks) (Wiggins and Parker 1997), the asilids *Lasiopogon prima* Adisoemarto-*L. septentrionalis* Lehr (Cannings 1997), the sphaerocerids *Rudolfina digitata* Marshall-*R. roskosnyi* (Roháček) and *Phthitia quadricercus* Marshall-*P. spinosa* (Collin) (Marshall 1997), a number of morphologically close and ecologically equivalent ant species in the Nearctic and Palaearctic regions (Francoeur 1997), and other taxa. Many of these species-level differences must reflect separation that predates the Pleistocene, but confirms the Miocene or Pliocene connection. North America and Eurasia were connected for 50 million years before they were separated in the Pliocene-Pleistocene.

Populations that might have differentiated in distinctive Beringian habitats would have had less than 5 ma to do so, yet species normally evolve relatively slowly (e.g. Matthews 1979; Elias 1994). Most of the Beringian, especially East Beringian, species thus probably represent relict refugial populations rather than recently derived regional endemics. Beringian components of more widespread populations nevertheless show interesting ranges and types of infraspecific variation. First, there are disjunctions between northwestern and eastern populations, between northern and southern North American populations, and north and south of treeline (see Disjunct Ranges above). Such separated subpopulations typically have 2 components (bicentric). In many instances, one part can be postulated to be derived from Beringia and the other from a southern refugium (e.g. Ball and Currie 1997 for many species of carabid beetles). Some other species have multicentric distributions, suggesting survival in a northern and in several southern refugia, and suggesting very strongly too that the species were widespread before Pleistocene events overtook them. Molecular studies have shown differences between the Yukon and more southern populations of the lygaeid bug *Geocoris bullatus* (Say) (Mulyk in Scudder 1997b). Similar bicentric and multicentric populations are known in other organisms apparently derived from more than one refugial source area (e.g. McPhail and Lindsey 1970 for many species of fish).

Finally, atypical findings may be especially interesting, or alternatively may suggest that taxonomic placement be re-evaluated. Vickery (1987, 1997) points out that a re-evaluation of the placement of the grasshopper genus *Bohemanella*, now considered a member of the tribe Podismini, corrected the conclusion that there had been a migration from the Nearctic region to the Palaearctic region, which would be the reverse of the direction taken by all other orthopteroïd species.

Overall, the most consistent pattern in the taxonomic evidence is the clear linkage between western Nearctic faunal elements and many Palaeartic species, as exemplified by taxonomic relationships at various levels (e.g. Mikkola et al. 1991; Currie 1997; Marshall 1997). Such relationships reflect the Beringian connections of the past.

Range Types. Current ranges, with fossil evidence of past ranges, allow strong inferences about the origins of Yukon species.

In a general Nearctic context, the proportion of Western species varies widely from group to group. Species confined to the Cordillera are especially prevalent in running waters. Such a western aspect to Yukon stoneflies and mayflies, for example, partly reflects the disjunction between eastern and western lotic habitats caused by the low relief of the central Great Plains and north to the Arctic Ocean, with slow, low-gradient streams and fine sediments, in contrast to the greater relief and rocky substrates to the west. Lentic habitats are not disjunct in the same way, and many more lentic species are transcontinental. Habitat availability thus influences the general character of potential source-groups for the Yukon fauna.

The ranges of Yukon species comprise 3 sets with respect to occurrence in Beringia. First, the current range limits of many species coincide closely with the boundaries of Beringia. Many East Beringian, East-West Beringian and Palaeartic-East Beringian species show this feature, together comprising more than 10% of known range types in groups where the data are more or less reliable (Table 7). Nearctic-West Beringian species show similar restriction but are much less numerous, suggesting that formerly Nearctic species spread westward into the Palaeartic region more rarely than species that originally were Palaeartic spread into East Beringia. Apparently, Nearctic Beringia during the Pleistocene was both small and species-poor compared to West Beringia (cf. Matthews and Telka 1997; Wiggins and Parker 1997).

The restricted ranges of the Beringian species suggest that they are specialized to arctic/subarctic conditions, the conditions of Pleistocene Beringia. As expected, tundra species are especially well represented in this group (Griffiths 1997; Lafontaine and Wood 1997; see Table 13). Nevertheless, the endemic species have not colonized similar arctic terrain elsewhere in North America. Moreover, many of the Palaeartic-East Beringian species live in a wider range of environments across the Palaeartic region than they do in Beringia itself (Wiggins and Parker 1997). Species at one time confined to Beringia (by inference, when it was a refugium) therefore must have been unable to spread farther because of inability to disperse, or inability to colonize. Similar restrictions to Beringia are well known in other organisms, especially in plants, in which a substantial fraction of the Yukon species are endemic to Beringia (Cody 1971, 1996). We know very little about the postglacial spread of species from Beringia (see Post-Pleistocene Development of the Fauna, below), but recent contact between species spreading from and into Beringia is suggested in some species by the existence of hybrids along the zone of contact (e.g. Cannings and Cannings 1985, 1997 for the dragonfly *Somatochlora sahlbergi*).

A second set of ranges, in contrast, does not include Beringia. These species are found in the southern Yukon only. Many such ranges belong to widespread Holarctic species (e.g. Scudder 1997b) or widespread Nearctic species (many authors; Fig. 11) that are not adapted to northern conditions, and presumably survived the glaciation in southern refugia. Other Nearctic species have Cordilleran ranges that only just penetrate the Yukon from the south (e.g. Fig. 10).

A third set of ranges comprises species with wider distributions that do include Beringia, as in many aphids and dytiscids (Footitt and Maw 1997; Larson 1997). The most charac-

teristic type here is a broad northern range (Figs. 7, 8). Such species occupy boreal (and often, too, subarctic and arctic) habitats across virtually the whole continent; most of them probably spread westward and northward into Beringia after deglaciation, but Pleistocene survival in Beringia might also have been possible. Fossil evidence can confirm whether Beringian species were actually in unglaciated Beringia, and indeed fossil evidence for carabid beetles suggests that 46% of species (rather than only the 13% established from current evidence) survived in the refugium (Ball and Currie 1997). Many species currently range more widely to the south, suggesting that they came at least largely from southern refugia (see also the discussion of Schwert and Ashworth 1988).

It is nonetheless necessary to draw inferences from such distributions with caution. The processes that have led to the current fauna of Canada as a whole and of the Yukon in particular have been extremely complex.

Post-Pleistocene Development of the Fauna. Changes affecting the Yukon fauna were especially dramatic during the final deglaciation, ending less than 10 000 years ago. These events changed climates and drainages very rapidly (cf. Matthews 1979; Danks 1981; information in Geological Survey of Canada 1987), echoing even more clearly the earlier repeated patterns of opening and closing of connections and the advance and retreat of the ice sheets.

Most insects are relatively mobile; their dispersal abilities would have allowed them to respond fairly quickly to the changed postglacial conditions of access and habitat suitability. Recently deglaciated terrain would have been suitable especially for species such as the carabid beetle *Asaphidion yukonense* Wickham, living in open areas with scattered moss patches (Elias 1994). As the climate warmed and the glaciers receded, herbs and shrubs (and eventually northern conifers) would have been restored, even quite close to the ice sheet (cf. Schwert and Ashworth 1988). The melt of the Laurentide glacier would have allowed access to the Yukon by species from the east, but of course such refugial source populations were much farther away from the Yukon than those immediately to the south in the Cordillera, even though the Cordilleran glaciers receded more slowly. West to east movement is currently favoured in North America by prevailing airstreams (the opposite direction to that required to reach the longitude of the Yukon from eastern North America), but the modern dominance of westerly winds probably would not have been as striking close to the huge remaining—and long-lived—ice accumulations and meltwater lakes at the end of the Pleistocene. That the Mackenzie Valley when forested would have been an important dispersal barrier to tundra forms is suggested by the many range disjunctions there (Danks 1981, 1993).

The eastward postglacial dispersal of arctic forms from Beringia across North America has been accepted on the basis of the ranges of many kinds of species that extend to varying degrees eastward (e.g. Freeman 1958 and other work reviewed by Danks 1981; Schwert and Ashworth 1988).

Many Cordilleran species, invading the Yukon from the south after deglaciation, have penetrated only part way into the Yukon. The proportion of such forms varies especially widely from group to group, evidently depending partly on habitat. Many of the aquatic species restricted in this way to the southern half of the Yukon live in lotic habitats, as in Plecoptera, associated in their southern ranges with mountain streams and similar habitats.

In some groups, essentially arctic species of the Yukon have penetrated southward along the Cordillera. For example, many species of dry-tundra Lepidoptera, such as several species of *Boloria*, extend southward in this way, albeit only narrowly along the dry east slope of

the Rocky Mountains (see maps in Scott 1996) and not in moister habitats. Because groups differ in whether species penetrate northward into the Yukon from the Cordillera, or southward in the Cordillera from the northern Yukon, the fauna of the Mackenzie Mountains includes characteristic arctic species of Lepidoptera (J.D. Lafontaine, pers. comm.), for example, but in the Dytiscidae has only boreal or Cordilleran species (D.J. Larson, pers. obs.).

The bulk of the Yukon fauna in many groups comprises widely distributed or broadly western boreal species, which appear to have invaded from the south (and east) from similar adjacent boreal areas. The history of the vast invasion by these many boreal forms from south of the ice front into their present northern ranges must have been extremely complex, guided or impeded by the terrain, and presumably later by the character of the biota that became established. However, we know very few details of this process (Downes 1997).

Typically, therefore, northwestern North American populations are derived from Beringian, southwestern (Cordilleran; and closer to the coast, Pacific) or southeastern sources, or combinations of 2 or more of these (compare the discussion above; McPhail and Lindsey 1970). In insects, specific information is most detailed for some species of carabid beetles and caddisflies (examples in Ball and Currie 1997; Wiggins and Parker 1997).

Nevertheless, the Canadian landscape was occupied by insects over a period of only a few thousand years following deglaciation, and the current picture is likely to be merely a stage in the development of equilibrium between the fauna and the climate, rather than an end result (Downes 1997; Matthews and Telka 1997; Schweger 1997). Notwithstanding evidence suggesting some integration in Yukon communities, we know little about the state of this equilibrium. Indeed, we understand the development of the fauna chiefly through preliminary faunal analysis. And we comprehend past and present dispersal routes only through a few particular effects, such as the canalization or interruption of leafhoppers and other insects by the wide Mackenzie Valley; or through a few isolated observations, as the range of a grasshopper ends in the Yukon on scattered favoured banks of warm gravel along the Eagle River, or as a low boreal butterfly is seen crossing the Richardson Mountains by the McDougall Pass. Nevertheless, the north-south orientated Richardson Mountains (and even the Mackenzie lowlands beyond) may, for a time, have partially blocked movement eastward out of Beringia, while to the southwest the St. Elias Mountains and their icefields separate the fauna of the southern Yukon almost completely from warmer, moister habitats of the extreme west coast. At the present state of knowledge, however, the development and nature of these large-scale faunal movements and interactions are largely unexplained.

Finally, a few Yukon species probably were introduced or have spread only recently into the Yukon (e.g. Foottit and Maw 1997 for several species of aphids associated with crops or introduced weeds; Marshall 1997 for 4 species of synanthropic sphaerocerids; Griffiths 1997 for the anthomyiid *Eutrichota lipsia* (Walker)).

Conclusions. Although taxonomic and ecological information for some taxa is very limited, many taxa from the Yukon are relatively well known, and for several groups different sets of evidence coincide and good comparative information is available from other regions. Such information, presented in earlier chapters and reviewed above, allows a synopsis of the Yukon fauna.

A first conclusion is that the components of the fauna reflect many different routes and origins. The Yukon has a long and complex environmental history, and has been a theatre for the interplay of evolution, movement and adaptation of a wide range of faunal elements.

One orientation to this diversity comes from its current features. Here is a markedly northern fauna, about one fifth of the insect fauna of Canada (Table 1), dominated by arctic,

subarctic and boreal elements. In many groups, species of northern boreal habitats are very prominently represented. The fauna is relatively diverse from an ecological perspective, occupying the many different microhabitats available in the Yukon habitat mosaic and eating many different foods. Some sections of the fauna are less well represented than in more temperate areas and, by analogy with well-known information for the arctic, climatic conditions therefore may be a more powerful force than biotic interactions. Nevertheless, there are phenological differences between related species and other traits usually taken as evidence of competition, so that most of these Yukon communities can be presumed to be more or less integrated.

Adaptations in several groups, and especially in species that are arctic, arctic-alpine or endemic to Beringia, are similar to those of arctic species in general, including cold-hardiness, long life cycles and wing reduction. Some Beringian endemic species show particular combinations of such characters, such as the remarkable set of modifications of some Beringian noctuid moths already noted.

The ecological character of the Yukon fauna confirms that northern and widespread groups that proved, as it were, to be preadapted to regional conditions dominate the fauna (see Table 6). As in the arctic, aquatic species are better represented than terrestrial ones, reflecting the relatively more stable and buffered conditions of many aquatic habitats compared to other habitats at high latitudes. Generalist predators are well represented, and so presumably are generalist saprophages, such as a variety of dipteran larvae, though detailed data on many taxonomically difficult groups of flies are not currently available. Conversely, herbivores, typically more specialized, are less well represented in the Yukon than farther south. Again, these trends appear to reflect the advantages in northern climates of relying on generally available foods.

Despite this northern aspect, southern elements are well represented too. Some southern Yukon habitats are relatively rich, and different life zones interdigitate (and there are few simple boundaries within the Territory), because the Yukon has so many mountains and is cut by river valleys. Certainly, the fauna is attenuated from south to north, but even so the change is gradual, and southern elements live on south-facing slopes and river valleys toward the north, while northern elements live on mountains or in cold water bodies in the southern Yukon. Some species are quite widely distributed in the Yukon. Species that live in relatively sheltered habitats such as in the soil (e.g. soil mites) and in the hyporheic zone of streams (e.g. some stoneflies) are not exposed to the full rigours of the Yukon climate. Certainly the fauna contains only about one-fifth of the Canadian species, but the Yukon is very much smaller than the rest of the country.

The current Yukon fauna also markedly reflects the influence of regional history. The most notable single feature is a strong connection at various times in the past with the Palaearctic region. Such a connection would have been especially clear when the Bering Strait area was forested millions of years ago, and later when it was exposed above the ocean during Pleistocene time; but even at present the distance there between Eurasia and North America is short, with some intervening islands, probably crossed relatively easily by mobile northern forms. The connection was reinforced, especially during glaciation, by the fact that the area—while still connected to the rest of Beringia (and very small relative to it)—was cut off by ice from the rest of North America. There is taxonomic evidence (see section above) of this affinity between the fauna of the Yukon Territory and that of Eurasia from the Tertiary (e.g. Matthews and Telka 1997) to the present, and there is considerable evidence for multiple exchanges over the long period of connection (e.g. Stewart and Ricker 1997). The occurrence of many Holarctic species, especially from the tundra, as well as species of

more restricted distribution centred on or limited to Beringia, to East Beringia, or to East Beringia in North America, attests to the repeated connections. Consequently, many species have passed from the Palaeartic region to the northwestern Nearctic region; a few species passed the other way.

Despite the changes in land connections and in the extent of ice cover during the Pleistocene, overall conditions in Beringia must have been relatively stable for a long time, because the area has been a centre of speciation for some groups of carabid beetles and moths (Ball and Currie 1997; Lafontaine and Wood 1997), and there are endemic species in other groups of butterflies and moths, leafhoppers, black flies, and many other taxa. Hence, a somewhat scattered but very significant number of endemic species persist in the Yukon, some 7% of the insect fauna (Table 7). As already noted, most of these species are tied to northern conditions or habitats, paralleling the late Pliocene and Pleistocene climates of Beringia. For example, endemic Lepidoptera are associated with dry tundra (Lafontaine and Wood 1997). Therefore, endemic species in the Yukon are best represented in northern groups, whereas few species of widespread and southern habitats are endemic (cf. Table 13). No dragonfly species is restricted to East Beringia. Presumably the Pleistocene refugium would have been too cold for most dragonflies (cf. Cannings and Cannings 1997), and indeed the glacial maxima in Beringia must have been bottlenecks for survival through which all of the fauna had to pass. The life-zone affinity and habitat requirements, and the specific history, of species in the fauna therefore are interwoven. An ability to live in cold climates is a key requirement of most species at present and also was in the past.

The mountain-associated fauna in the Yukon is of particular interest. The highest mountains, of the St. Elias range, are in the southern Yukon; their peaks (to about 6000 m) are far above the limit for arthropod life. The elevation of treeline, and of the mountains themselves, decreases steadily toward the arctic coast, until the "alpine" and "arctic" features eventually merge at the arctic coastal plain. As might be expected, the fauna of these mountains includes a substantial number of arctic-alpine species, characteristic of the northern Yukon (cf. Lafontaine and Wood 1997). Several of these species have typical arctic adaptations such as reduced wings (see Wing Loss...). Some of them evidently had populations also to the south of the ice sheets, which were able to survive on southern mountains as the ice receded, leaving relict populations in the Cordillera in the west or in the Appalachians in the east (cf. Downes 1997). Information from ranges, already reviewed, suggests that another fraction of the mountain fauna—with less marked arctic characteristics, though adapted for example to cold mountain streams—survived glaciation only in the south and has invaded the Yukon along the Cordillera, but has not penetrated into the northern Yukon. These elements of the fauna would certainly reward further study.

In summary, the insect fauna of the Yukon Territory, though clearly northern, is a relatively rich and distinctive one. These features stem from the complex topography and wide range of habitats, giving many suitable places for insects to live, despite the high latitude and the predominantly subarctic and boreal character. The fauna also owes its distinctiveness and richness to a history of repeated connections to the Palaeartic region and to the intermittent interruption of wider North American connections. The fauna has some essentially Eurasian (rather than North American) species (cf. Griffiths 1997), and apparently persistent species that survived glaciation in the Beringian refugium, in addition to many Nearctic postglacial invaders of various types from both southwestern and southeastern (though chiefly boreal) North American sources. It is worth emphasizing that the history of environmental suitability and dispersal avenues in this area has interacted with the characteristics and origins of different taxa to produce many different outcomes. The

Yukon fauna is a complex mixture that cannot be characterized adequately by a few sweeping generalizations.

Future Prospects. This chapter summarizes current perspectives on the Yukon fauna, but much remains to be discovered. Some of the facts, lost in history, will always remain unknown, but the increasing interest in the region and its increasing accessibility hold promise for additional discoveries.

Additional survey and collecting is required in many families not yet collected in any detail. It is also required in most groups of arthropods treated here to provide broader coverage of the Yukon beyond sites easily accessible by road and river. It is also necessary to obtain records for comparison from Alaska, the Northwest Territories and, especially for some groups, eastern Siberia and the Russian Far East.

Adequate systematic knowledge of groups that include Yukon representatives is the essential basis for the study of diversity, so that the continued description and evaluation of these northern forms is required. Taxonomic research on Nearctic, Palaearctic and potential Holarctic insect species in the Yukon Territory has invariably yielded fascinating findings of endemism, adaptation, disjunction, or other evidence about faunal evolution in the crucible of Beringian history.

Ecological studies related to adaptations, life-cycle control, cold-hardiness, habitat use and competition are also required. Such studies allow us to ask whether, following the major Pleistocene and post-Pleistocene disturbances, the Yukon fauna is yet fully integrated with current climatic and biotic influences. The presence or absence of such an equilibrium will be easier to assess when more of the essential collecting and taxonomic research has been done.

Acknowledgements

We thank the many authors whose informative contributions to this book made a concluding chapter feasible, and the individual systematists (identified in Table 1, footnote 3) who helped to update the numbers of known Canadian and North American species in certain taxa. We are also grateful to George E. Ball for his helpful comments on the manuscript.

References

- Anderson, R.S. 1997a. An overview of the beetles (Coleoptera) of the Yukon. pp. 405–444 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- 1997b. Weevils (Coleoptera: Curculionioidea, excluding Scolytinae and Platypodinae) of the Yukon. pp. 523–562 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Arnett, R.H., Jr. 1990. Present and future of systematics of the Coleoptera in North America. pp. 165–173 in M. Kosztarab and C.W. Schaefer (Eds.), *Systematics of the North American Insects and Arachnids: Status and Needs*. Virginia Agricultural Experiment Station Information Series 90–1. 247 pp.
- Babb, T.A. and L.C. Bliss. 1974. Susceptibility to environmental impact in the Queen Elisabeth Islands. *Arctic* 27:234–237 and map.
- Ball, G.E. 1963. The distribution of the species of the subgenus *Cryobius* (Coleoptera: Carabidae, *Pterostichus*). pp. 133–151 in J.L. Gressitt (Ed.), *Pacific Basin Biogeography*. Bishop Museum Press, Honolulu (Symp. 10th Pacific Sci. Congr. 1961). 563 pp.
- Ball, G.E. and D.C. Currie. 1997. Ground beetles (Coleoptera: Trachypachidae and Carabidae) of the Yukon: geographical distribution, ecological aspects, and origin of the extant fauna. pp. 445–489 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Behan-Pelletier, V.M. 1997. Oribatid mites (Acari: Oribatida) of the Yukon. pp. 115–149 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Belton, E.M. and P. Belton. 1990. A review of mosquito collecting in the Yukon. *J. ent. Soc. Br. Columb.* 87:35–37.
- Bousquet, Y. (Ed.). 1991. Checklist of Beetles of Canada and Alaska. *Res. Brch Agric. Can. Publ.* 1861/E. 430 pp.

- Cannings, R.A. 1997. Robber flies (Diptera: Asilidae) of the Yukon. pp. 637–662 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Cannings, S.G. and R.A. Cannings. 1985. The larva of *Somatochlora sahlbergi* Tryböm, with notes on the species in the Yukon Territory, Canada (Anisoptera: Corduliidae). *Odonatologica* 14:319–330.
- 1997. Dragonflies (Odonata) of the Yukon. pp. 169–200 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Cobb, D.G. and J.F. Flannagan. 1980. The distribution of Ephemeroptera in northern Canada. pp. 155–166 in J.F. Flannagan and K.E. Marshall (Eds.), *Advances in Ephemeroptera Biology*. Plenum, New York. 552 pp.
- Cody, W.J. 1971. A phytogeographic study of the floras of the continental Northwest Territories and Yukon. *Naturaliste can.* 98:145–158.
- 1996. *Flora of the Yukon*. National Research Council Research Press, Ottawa. 643 pp.
- Corbet, P.S. and H.V. Danks. 1973. Seasonal emergence and activity of mosquitoes in a high arctic locality. *Can. Ent.* 105:837–872.
- Cowan, C.A. and M.W. Oswood. 1984. Spatial and seasonal associations of benthic macroinvertebrates and detritus in an Alaskan subarctic stream. *Polar Biol.* 3:211–215.
- Currie, D.C. 1997. Black flies (Diptera: Simuliidae) of the Yukon, with reference to the black-fly fauna of northwestern North America. pp. 563–614 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Danks, H.V. 1971. Overwintering of some north temperate and arctic Chironomidae. II. Chironomid biology. *Can. Ent.* 103:1875–1910.
- (Ed.) 1979. Canada and its Insect Fauna. *Mem. ent. Soc. Can.* 108. 573 pp.
- 1981. Arctic Arthropods. A Review of Systematics and Ecology with Particular Reference to the North American Fauna. Entomological Society of Canada, Ottawa. 608 pp.
- 1986. Insect-plant interactions in arctic regions. *Rev. Ent. Quebec.* 31:52–75.
- 1987. Insect Dormancy: an Ecological Perspective. Biological Survey of Canada (Terrestrial Arthropods), Ottawa. 439 pp.
- 1988. Systematics in support of entomology. *A. Rev. Ent.* 33:271–296.
- 1990. Arctic insects: instructive diversity. pp. 444–470, Vol. II in C.R. Harington (Ed.), *Canada's Missing Dimension: Science and History in the Canadian Arctic Islands*. Canadian Museum of Nature, Ottawa. 2 vols, 855 pp.
- 1991. Winter habitats and ecological adaptations for winter survival. pp. 231–259 in R.E. Lee Jr. and D.L. Denlinger (Eds.), *Insects at Low Temperature*. Chapman and Hall, New York, London. 513 pp.
- 1993. Patterns of diversity in the Canadian insect fauna. pp. 51–74 in G.E. Ball and H.V. Danks (Eds.), *Systematics and Entomology: Diversity, Distribution, Adaptation and Application*. *Mem. ent. Soc. Can.* 165. 272 pp.
- 1994a. Regional diversity of insects in North America. *Am. Ent.* 41:50–55.
- 1994b. Insect life-cycle polymorphism: current ideas and future prospects. pp. 349–365 in H.V. Danks (Ed.), *Insect Life-cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*. Kluwer Academic Publishers, Dordrecht. 378 pp.
- 1996. The wider integration of studies on insect cold-hardiness. *Eur. J. Ent.* 93:383–403.
- in press. Terrestrial arthropods in the Nearctic Region: diversity and resources for study. in K.C. Kim (Ed.), *Biodiversity and Taxonomy of Insects and Arachnids: A Global Perspective*. Universal Book Services, Leiden.
- Danks, H.V. and R.G. Footitt. 1989. Insects of the boreal zone of Canada. *Can. Ent.* 121:626–677.
- Danks, H.V., O. Kukal, and R.A. Ring. 1994. Insect cold-hardiness: insights from the arctic. *Arctic* 47:391–404.
- Danks, H.V. and D.R. Oliver. 1972. Seasonal emergence of some high arctic Chironomidae (Diptera). *Can. Ent.* 104:661–686.
- Danks, H.V. and D.D. Williams. 1991. Arthropods of springs, with particular reference to Canada: synthesis and needs for research. pp. 203–217 in D.D. Williams and H.V. Danks (Eds.), *Arthropods of Springs, with Particular Reference to Canada*. *Mem. ent. Soc. Can.* 156. 217 pp.
- Darlington, P.J. 1943. Carabidae of mountains and islands: data on the evolution of isolated faunas, and on atrophy of wings. *Ecol. Monogr.* 13:37–61.
- Dondale, C.D. and J.H. Redner. 1997. Spiders (Araneae) of the Yukon. pp. 73–113 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.
- Dort, W., Jr. 1972. Stadial subdivisions of early Pleistocene glaciations in central United States—a developing chronology. *Boreas* 1:56–61.
- Douglas, G.W. 1974. Montane zone vegetation of the Alsek River region, southwestern Yukon. *Can. J. Bot.* 52:2505–2532.
- Downes, J.A. 1962. What is an arctic insect? *Can. Ent.* 94:143–162.
- 1964. Arctic insects and their environment. *Can. Ent.* 96:280–307.
- 1965. Adaptations of insects in the arctic. *A. Rev. Ent.* 10:257–274.
- 1970. The feeding and mating behaviour of the specialized Empidinae (Diptera); observations on four species of *Rhamphomyia* in the high arctic and a general discussion. *Can. Ent.* 102:769–791.
- 1997. Introduction to the insects of the Yukon. pp. 7–11 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon*. Biological Survey of Canada (Terrestrial Arthropods), Ottawa.

- Elias, S.A. 1994. Quaternary Insects and their Environments. Smithsonian Institution, Washington. 284 pp.
- Elias, S.A., S.K. Short, C.H. Nelson, and H.H. Birks. 1996. Life and times of the Bering land bridge. *Nature* 382:60–63.
- Fink, J. and G.J. Kukla. 1977. Pleistocene climates in central Europe: at least 17 interglacials after the Olduvai event. *Quaternary Res.* 7:363–371.
- Finnamore, A.T. 1997. Aculeate wasps (Hymenoptera: Aculeata) of the Yukon, other than Formicidae. pp. 867–900 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Footitt, R.G. and E. Maw. 1997. Aphids (Homoptera: Aphidoidea) of the Yukon. pp. 387–404 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Francoeur, A. 1997. Ants (Hymenoptera: Formicidae) of the Yukon. pp. 901–910 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Freeman, T.N. 1958. The distribution of arctic and subarctic butterflies. *Proc. 10th int. Congr. Ent.* (Montreal 1956) 1:659–672.
- Geological Survey of Canada. 1987. Paleogeography of Northern North America. Map 1703A (3 sheets, 18 000–12 000, 11 000–8400, and 8000–5000 years ago, based on paleogeography by A.S. Dyke and V.K. Prest). Geological Survey of Canada, Ottawa.
- Griffiths, G.C.D. 1997. Anthomyiid flies (Diptera: Anthomyiidae) of the Yukon. pp. 687–722 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Hamilton, K.G.A. 1983. Introduced and native leafhoppers common to the Old and New Worlds (Rhynchota: Homoptera: Cicadellidae). *Can. Ent.* 115:473–511.
- 1997. Leafhoppers (Homoptera: Cicadellidae) of the Yukon: dispersal and endemism. pp. 337–375 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Hanski, I. 1988. Four kinds of extra long diapause in insects: a review of theory and observations. *Annls zool. fenn.* 25:37–53.
- Harper, P.P. and F. Harper. 1997. Mayflies (Ephemeroptera) of the Yukon. pp. 151–167 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Heliövaara, K. and R. Vaisänen. 1984. The biogeographical mystery of alternate-year populations of *Aradus cinnamomeus*. *J. Biogeogr.* 11:491–499.
- 1986. Bugs in bags: intraspecific competition affects the biogeography of the alternate-year population of *Aradus cinnamomeus* (Heteroptera). *Oikos* 47:327–334.
- 1988. Periodicity of *Aradus cinnamomeus* in northern Europe. *Ent. Tidskr.* 109:53–58.
- Hodges, R.W. et al. (Eds.). 1983. Check List of the Lepidoptera of America North of Mexico including Greenland. E.W. Classey Ltd. and Wedge Entomological Research Foundation, London. 284 pp.
- Hynes, H.B.N. 1988. Biogeography and origins of the North American stoneflies (Plecoptera). pp. 31–37 in J.A. Downes and D.H. Kavanaugh (Eds.), *Origins of the North American Insect Fauna. Mem. ent. Soc. Can.* 144. 168 pp.
- Irving, E. 1977. Drift of the major continental blocks since the Devonian. *Nature* 270:304–309.
- Kosztarab, M. and C.W. Schaefer (Eds.). Systematics of the North American Insects and Arachnids: Status and Needs. Virginia Agricultural Experiment Station Information Series 90–1. 247 pp.
- Lafontaine, J.D., K. Mikkola, and V.S. Kononenko. 1983. A revision of the genus *Xestia* subg. *Schoyenia* Auriv. (Lepidoptera: Noctuidae), with descriptions of four new species and a new subspecies. *Entomologica scand.* 14:337–369.
- 1987. A revision of the genus *Xestia* Hbn. subgenus *Pachnobia* Gn. (Lepidoptera: Noctuidae), with descriptions of two new subspecies. *Entomologica scand.* 18:305–331.
- Lafontaine, J.D. and D.M. Wood. 1988. A zoogeographic analysis of the Noctuidae (Lepidoptera) of Beringia, and some inferences about past Beringian habitats. pp. 109–123 in J.A. Downes and D.H. Kavanaugh (Eds.), *Origins of the North American Insect Fauna. Mem. ent. Soc. Can.* 144. 168 pp.
- 1997. Butterflies and moths (Lepidoptera) of the Yukon. pp. 723–785 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Larson, D.J. 1994. Revision of North American *Agabus* Leach (Coleoptera: Dytiscidae): *lutosus*-, *obsoletus*-, and *fuscipennis*-groups. *Can. Ent.* 126:135–181.
- 1997. Dytiscid water beetles (Coleoptera: Dytiscidae) of the Yukon. pp. 491–522 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Marshall, S.A. 1997. Sphaerocerid flies (Diptera: Sphaeroceridae) of the Yukon. pp. 663–685 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Matthews, J.V., Jr. 1979. Tertiary and Quaternary environments: historical background for an analysis of the Canadian insect fauna. pp. 31–86 in H.V. Danks (Ed.), *Canada and its Insect Fauna. Mem. ent. Soc. Can.* 108. 573 pp.
- Matthews, J.V., Jr. and A. Telka. 1997. Insect fossils from the Yukon. pp. 911–962 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- McCafferty, W.P. 1985. The Ephemeroptera of Alaska. *Proc. ent. Soc. Wash.* 87:381–386.
- 1996. The Ephemeroptera species of North America and index to their complete nomenclature. *Trans. Am. ent. Soc.* 122:1–54.

- McPhail, J.D. and C.C. Lindsey. 1970. Freshwater Fishes of Northwestern Canada and Alaska. *Bull. Fish. Res. Bd Can.* 173. 381 pp.
- Merritt, R.W. and K.W. Cummins (Eds.). 1989. An Introduction to the Aquatic Insects of North America. Kendall/Hunt, Dubuque, Iowa. 441 pp.
- Mikkola, K. 1976. Alternate-year flight of northern *Xestia* species (Lepidoptera) and its adaptive significance. *Annls ent. fenn.* 42:191–199.
- Mikkola, K. and V.S. Kononenko. 1989. Flight years of the alternate-year *Xestia* moths (Lepidoptera) in north-eastern Siberia—a character from the Ice Ages? *Nota Lepid.* 12:144–152.
- Mikkola, K., J.D. Lafontaine, and V.S. Kononenko. 1991. Zoogeography of the Holarctic species of the Noctuidae (Lepidoptera): importance of the Beringian refuge. *Entomologica fenn.* 2:157–173.
- Nylin, S. 1994. Seasonal plasticity and life-cycle adaptations in butterflies. pp. 41–67 in H.V. Danks (Ed.), *Insect Life-cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*. Kluwer Academic Publishers, Dordrecht. 378 pp.
- Oliver, D.R. and M.E. Dillon. 1997. Chironomids (Diptera: Chironomidae) of the Yukon Arctic North Slope and Herschel Island. pp. 615–635 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Oswald, E.T. and B.N. Brown. 1990. Vegetation Establishment During 5 Years Following Wildfire in Northern British Columbia and Southern Yukon Territory. Forestry Canada, Pacific and Yukon Region Information Report BC-X-320. 46 pp.
- Oswood, M.W., L.K. Miller, and J.G. Irons III. 1991. Overwintering of freshwater benthic macroinvertebrates. pp. 360–375 in R.E. Lee Jr. and D.L. Denlinger (Eds.), *Insects at Low Temperature*. Chapman and Hall, New York, London. 513 pp.
- Reeves, B.O.K. 1973. The nature and age of the contact between the Laurentide and Cordilleran ice sheets in the western interior of North America. *Arct. Alp. Res.* 5:1–16.
- Roff, D.A. 1990. The evolution of flightlessness in insects. *Ecol. Monogr.* 60: 389–421.
- Ross, H.H. 1970. The ecological history of the Great Plains: evidence from grassland insects. pp. 225–240 in W. Dort Jr. and J.K. Jones Jr. (Eds.), *Pleistocene and Recent Environments of the Central Great Plains*. Univ. Kansas Press, Lawrence. 433 pp.
- Samways, M.J. 1994. *Insect Conservation Biology*. Chapman and Hall, London. 358 pp.
- Schweger, C.E. 1997. Late Quaternary palaeoecology of the Yukon: a review. pp. 59–72 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Schwert, D.P. and A.C. Ashworth. 1988. Late Quaternary history of the northern beetle fauna of North America: a synthesis of fossil and distributional evidence. pp. 93–107 in J.A. Downes and D.H. Kavanaugh (Eds.), *Origins of the North American Insect Fauna. Mem. ent. Soc. Can.* 144. 168 pp.
- Scott, J.A. 1986. *The Butterflies of North America. A Natural History and Field Guide*. Stanford Univ. Press, Stanford. 583 pp.
- Scudder, G.G.E. 1997a. Environment of the Yukon. pp. 13–57 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- 1997b. True bugs (Heteroptera) of the Yukon. pp. 241–336 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Stewart, K.W., R.L. Hassage, S.J. Holder, and M.W. Oswood. 1990. Life cycles of six stonefly species (Plecoptera) in subarctic and arctic Alaska streams. *Ann. ent. Soc. Am.* 83:207–214.
- Stewart, K.W. and W.E. Ricker. 1997. Stoneflies (Plecoptera) of the Yukon. pp. 201–222 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Van Donk, J. 1976. O¹⁸ record of the Atlantic Ocean for the entire Pleistocene Epoch. *Mem. geol. Soc. Am.* 145:147–163.
- Vickery, V.R. 1987. The northern Nearctic Orthoptera: their origins and survival. 52, pp. 581–591 in B. Baccetti (Ed.), *Evolutionary Biology of the Orthopteroid Insects*. E. Horwood, Ltd., Chichester, England.
- 1997. Orthopteroid insects (Orthoptera) of the Yukon. pp. 223–239 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Wiggins, G.B. and C.R. Parker. 1997. Caddisflies (Trichoptera) of the Yukon, with analysis of the Beringian and Holarctic species of North America. pp. 787–866 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Wilson, S.R. 1997. Delphacid planthoppers (Homoptera: Fulgoroidea: Delphacidae) of the Yukon. pp. 377–385 in H.V. Danks and J.A. Downes (Eds.), *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa.
- Wipking, W. and C. Mengelkoch. 1994. Control of alternate-year flight activities in high-alpine Ringlet butterflies (*Erebia*, Satyridae) and Burnet moths (*Zygaena*, Zygaenidae) from temperate environments. pp. 313–347 in H.V. Danks (Ed.), *Insect Life-cycle Polymorphism: Theory, Evolution and Ecological Consequences for Seasonality and Diapause Control*. Kluwer Academic Publishers, Dordrecht. 378 pp.
- Wood, D.M., P.T. Dang, and R.A. Ellis. 1979. The Mosquitoes of Canada (Diptera: Culicidae). The insects and arachnids of Canada Part 6. *Agric. Can. Publ.* 1686. 390 pp.
- Wright, H.E., Jr. 1976. The dynamic nature of Holocene vegetation, a problem in paleoclimatology, biogeography and stratigraphy nomenclature. *Quaternary Res.* 6:581–596.